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THE HISTORY OF THE *PINUS SYLVESTRIS* TREELINE AT CREAG FHIACLACH, INVERNESS-SHIRE

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A thesis submitted for the degree of Doctor of Philosophy

1996

Abstract

The history of the *Pinus sylvestris* L. treeline at Creag Fhiaclach was investigated using a palynological approach. A modern pollen rain study demonstrated that the current treeline was detectable from a significant ($p < 0.0001$) reduction in the *Pinus/(Pinus + Calluna vulgaris* (L.) Hull) pollen quotient. Heath vegetation typically has a P*100/(P+C) pollen quotient of less than 30%. Quotients higher than 30% represent *Pinus* woodland. A three year study on variation in *Calluna* flowering with altitude showed that the relative reduction in the *Pinus* pollen component at the treeline is caused primarily by changes in the density of *Calluna* flowering rather than *Pinus* pollen influx. The results have implications for the design of palynological studies, indicating the importance of replication, as well as aiding interpretation of sub-fossil pollen data.

Five replicate cores from six altitudes spanning the treeline were subjected to pollen analysis for the historical investigation. Twenty six palynomorphs including four Rhizopod taxa were described. Discriminant analysis was used in addition to quotients to classify the sub-fossil pollen assemblages as either heath or forest types. The palynological data were reduced using PCA and RDA and showed that a higher treeline may have been previously present at the more sheltered southern end of the treeline. However, an alternative hypothesis, of pollen assemblages similar to those of *Pinus* forest being produced by relatively infertile *Juniperus communis* L. canopies, was also tested by looking at the pollen spectra from transects across *Juniperus communis* patches. Dense patches of *Juniperus communis* result in pollen assemblages which cannot be distinguished from those of *Pinus sylvestris* woodland.

^{210}Pb and ^{14}C dates, while indicating stratigraphic validity, gave conflicting evidence for the ages of the peat deposit at Creag Fhiaclach. Evidence from dendrochronology on the site suggests that the ^{14}C dates are more correct and that the peat deposit dates from 1227-940 BP.

A model of pollen distribution at the treeline on the basis of modern pollen deposition is proposed. The relative stability of this treeline poses interesting questions about how the treeline established and the inertia of this type of vegetation boundary to changes in climate.

Acknowledgements

I would like to warmly thank my supervisor, Dr. Colin Legg for his encouragement, interest, advice and support during the preparation of this thesis.

Special thanks are due to Drs. Gus MacKenzie and Gordon Cook at the Scottish Universities Reactor Research Centre in East Kilbride for access to facilities and assistance in the radiocarbon and ^{210}Pb dating. Similarly, Dr. Andy Dugmore provided facilities for both the tephra chronology and assistance with the peat X-rays. Assistance of Messrs Derek Scott, Andy Gray and John Morman in the Institute of Ecology and Resource Management is also acknowledged. Mr. John Finlay provided the photographs of the rhizopods.

Profs. John Birks, John Grace and Jon Pilcher and Drs. Richard Tipping and Valerie Hall were indulgent to my many questions and freely gave the benefit of their experience, enthusiasm and friendship.

Mr. David Carstairs of Scottish Natural Heritage is thanked for permission to use the site at Creag Fhiaclach and for his continued interest in this project.

Dr. Brian Coppins at the Royal Botanic Gardens Edinburgh, is thanked for verifying the identification of the lichens from Creag Fhiaclach.

My colleagues in the Institute of Ecology and Resource Management are thanked for their humour and forbearance, making my time at Edinburgh stimulating and rewarding.

The Department of Education (Northern Ireland) provided a scholarship, without which this project could not have been undertaken.

Dr. Laszlo Nagy proof read this thesis and provided much needed moral support.

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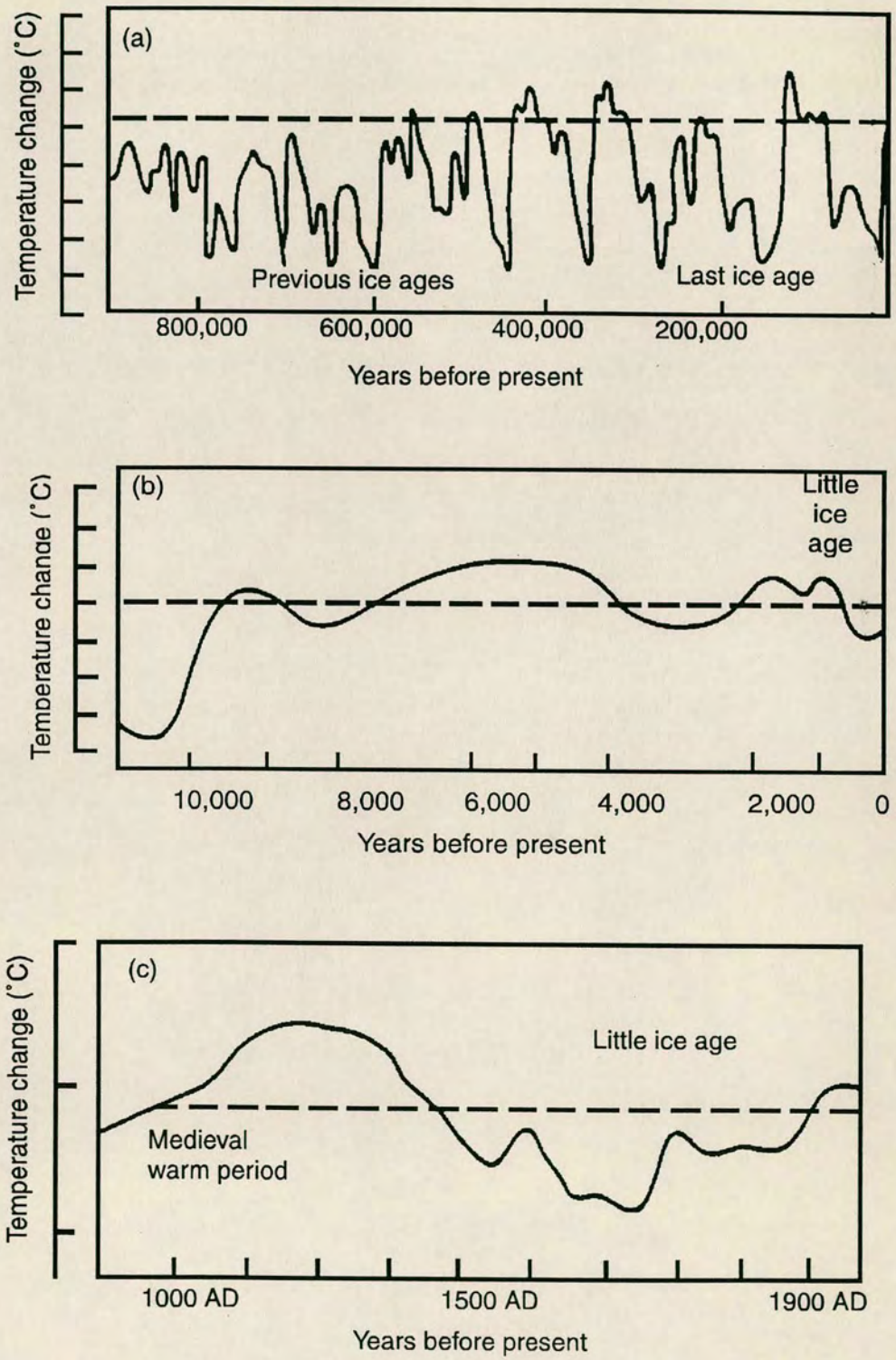
Introduction

1.1 Background

The earth's climate is and has been constantly changing over a number of time scales (Figure 1.1). On shorter time scales the vagaries of climate have caused enormous difficulties in identifying trends. An increase in the mean global air temperature of approximately 0.6 °C since AD 1860 is now broadly accepted (Jones *et al.*, 1986). This increase in the mean global air temperature is coincident with increased atmospheric concentrations of CO_2, CH_4, N_2O and CFC's through industrialisation (Watson *et al.*, 1990). Most notable is the increased concentration of CO_2 which has risen from 280 ppm in pre-industrial times, to 350 ppm today and is predicted by some scenarios to increase to 560 ppm by the late twenty-first century (Watson *et al.*, 1990). The causal relationship between increased concentrations of radiatively active gases and increasing air temperatures is still tenuous. Despite the lack of conclusive evidence there is concern that if CO_2 concentration is driving global climate warming then, as undeveloped nations make the transition to industrialised societies, the increase in mean temperatures and associated climate variables will impact heavily on all biotic natural resources.

Reflecting this concern, considerable research effort has been invested in predicting the nature, degree and direction of future climate changes. While increasing mean global air temperatures are frequently predicted, there is still considerable uncertainty on the degree of increase at the regional level (Houghton *et al.*, 1990). Predicted changes for the next century vary from 0.9-1.5 °C in Scandinavia (Santer *et al.*, 1990), to 2-6 °C in North America (Bonan *et al.*, 1990), with increases expected to be greater at higher latitudes because of feedback effects caused by to albedo (Kukla & Kukla, 1974; Hansen *et al.*, 1988). Data for the British Isles suggest that summer temperatures will increase by 1.1 °C and winter temperatures by 1.2-1.7 °C with greater warming in Scotland (Wigley & Raper, 1992).

Figure 1.1: Schematic diagrams of global temperature variations (in 1 °C) since the Pleistocene on three time-scales: (a) the last million years, (b) the last ten thousand years, and (c) the last thousand years. The broken line nominally represents conditions near the beginning of the twentieth century. After Houghton *et al.* (1990).



Palaeoclimatic reconstructions have shown that there were analogous rates of change in the mid-Holocene. These rates of change have been shown to have substantially altered the distribution of plant and animal species (Huntley & Birks, 1983; Birks, 1990). The most conspicuous response of plants to climatic change is migration (Huntley, 1991). Climatic variations of large amplitude may cause rapid long-distance range boundary movements of individual species. Rapid boundary movements can also occur in response to much smaller changes in climate (Prentice, 1986).

Overpeck *et al.* (1991) have used climate-pollen response surfaces to model vegetation distribution under higher future temperature scenarios. Elevational changes in plant distribution are much more sensitive to small variations in climate than latitudinal changes (Davis & Botkin, 1985) and vegetation in mountainous regions characteristically shows distinct zonation in response to steep environmental gradients (Crawford, 1989). Some of the predicted responses to a warmer environment are already observable in high alpine vegetation belts (Grabherr *et al.*, 1994) and recent rises in treelines across the northern hemisphere have been correlated to post-industrial temperature increase (Innes, 1991), though these have not yet reached the elevation of the mid-Holocene optimum.

Any hypothesis on climatically driven changes in plant distribution must be shown to be consistent with events in climatology and plant population ecology (Prentice, 1986). Climatic changes over Milankovitch time scales (10^3 - 10^5 years) and subsequent plant responses are reasonably well understood. Changes in plant communities over millennial times scales are also well documented, however the statistical vagaries of climate over these time scales are poorly understood. Climatic changes over the scale of available meteorological records (10 - 10^2 years) are well understood, but, there has been a dearth of research on the associated changes in vegetation over these time scales. These are the time scales of current interest in climate change modelling.

This study describes the changes in the *Pinus sylvestris* treeline at Creag Fhiaclach in the Cairngorms, Scotland, over a temporal scale of 10-10^3 years. Vegetation responses to past climate change can be studied retrospectively by utilising fossil records (Prentice, 1986; Adams & Woodward, 1992). Responses within the 10-10^2 time scales bridge the gap between a time scale of meteorological observation and the resolution possible from

fine scale palaeoecological research, providing an opportunity for an applied palaeoecological approach to ecological questions (Birks, 1993). The majority of previous research on climatically driven changes in treeline elevation in the northern hemisphere have used macrofossils. However, the distribution of macrofossils is patchy in both time and space and is dependant on prevailing conditions for preservation. In particular, at high altitudes peat accumulation rates are very slow and preservation is therefore poor. This is particularly true at Creag Fhiaclach. Therefore, this investigation into treeline fluctuations at Creag Fhiaclach used palynological techniques. It should be remembered throughout the remainder of this thesis that the palynological approach is used as a tool to answer an essentially ecological question. The objectives of this thesis were to:

1. calibrate the relationship between the present treeline and modern pollen deposition,
2. use this calibration to investigate past treeline fluctuations,
3. investigate the factors determining the position of the treeline,
4. predict possible future treeline fluctuations.

For the purposes of this thesis a treeline is defined after Wardle (1974) as the upper limit of 'trees, krummholtz and scrub growth over two metres tall'. Nomenclature throughout follows Moore, Webb & Collinson (1991) for pollen grains and spores, Clapham, Tutin & Moore (1987) for vascular plants, Smith (1978) for bryophytes and Purvis *et al.* (1992) for lichens, unless specified otherwise.

1.2 Detecting variation in treeline elevation using palynology

1.2.1 Introduction

Trees are tightly coupled to air temperature (Grace, 1983) and the upper treeline has been cited as the most temperature sensitive zonation boundary in nature (Tikhomirov, 1979). The upper treeline advances to higher elevations during ameliorated climatic conditions and retreats in inclement environments. Treelines have thus been used empirically to study climatic trends and analogous palaeoclimatic reconstructions. This literature review shall first look at the climatic restrictions on treeline advances. In considering this, particular attention will be given to coniferous treelines in the northern hemisphere. Detection of treelines using palynological techniques is then considered through a discussion of pollen distribution and representation at treelines. Finally, previous

palynological literature on altitudinal treeline studies in north America and Britain are considered, with both palynological and dendrochronological evidence for previous treeline fluctuations in the Cairngorms being discussed.

1.2.2 Links between treelines and climate

Grace (1987) stated that the climatic limits to plant distribution are physiologically determined through disruption of some part of the plant's life-cycle. Climate influences four key environmental factors for plant growth; temperature, wind speeds, gas exchange and hydrology. Of these the single most important determinant of life-cycle processes at the treeline is temperature. Temperature shows a gradual decrease with altitude because of reduced insolation. Treeline sensitivity to temperature is largely through regulation of the carbon balance of individual trees; tree performance, measured as biomass, height and diameter increments, generally declines with altitude. The duration of temperatures above a threshold (growing season) must be long enough to allow sufficient assimilation of carbon to maintain respiration throughout the remainder of the year and in at least some years allow reproduction. Empirical evidence from many treelines has shown that this altitude generally correlates with the 10 °C summer isotherm (Tranquillini, 1979). This generalisation also holds for arctic treelines (Mikola, 1962; Bryson 1966).

The temperature environment experienced by trees cannot be directly predicted from standard meteorological data as leaf temperatures at high altitudes are a function of wind speeds (exposure) in addition to net radiation fluxes (Körner & Larcher 1988). While temperature is thought to be the most important determinant in regions of continental climate, wind speed (exposure) is thought to be the controlling factor in oceanic regions (Pears, 1967). Grace (1977, 1983) proposed that taller vegetation is more tightly coupled to air temperatures because it acts aerodynamically as a rough surface and the air is well mixed. Shorter vegetation is smoother and the air above it is less well mixed. Both Wilson *et al.* (1987) and James *et al.*'s (1994) work at Creag Fhiaclach support this. Wilson *et al.* (1987) concluded that average meristem temperatures were higher in short vegetation compared with taller vegetation, an effect that is reduced with increasing wind speeds at very high altitudes. The effective lapse rate of meristem temperatures was zero but, diurnal amplitude of temperature was greater for short vegetation. Thus, the elevational range differs between life forms, with herbs and shrubs able to maintain

adequate carbon balances to higher elevations than trees. Additional support for this hypothesis is found in the work of James *et al.* (1994). Also working at Creag Fhiaclach, they found a significant difference in meristem tissue temperature of potted *Pinus* saplings compared with air temperatures at the treeline. Inevitably this difference was due to greater agitation of the boundary layer around the saplings occurring above the treeline.

In addition to reducing temperature, wind can also be a major stress and determinant of prevalent life-forms through direct morphological and physiological effects (Grace 1977; 1983). Wind can also affect gas exchange in addition to the temperature environment of the leaf hence regulating the rate of photosynthesis. Wind can also directly influence the carbon balance through frost pruning and loss of branches in gales.

Seasonal variation in water relations at the treeline is caused by increased radiation in summer and unavailability of frozen water in winter. Winter drought stress, caused by cuticular water loss has been hypothesised by Tranquillini (1979) to be a determining factor for altitudinal position of the treeline in the Alps. However, drought stress through cuticular water loss has been shown by Grace (1990) to be an unlikely determinant of treeline elevation for *Pinus sylvestris* in Scotland. The slightly higher leaf transpiration rates in krummholtz and isolated trees were shown to be caused by stomatal dysfunction through abrasion damage (Grace 1990; van Gardingen *et al.* 1991) and not by poor cuticle development. The level of damage found was not thought to be sufficient to be evoked as a mechanism limiting the altitudinal limit of tree growth.

However, treeline elevation may be modified by factors not directly related to climate. For example, Hättenschwiler & Körner (1995) tentatively suggested that the *Pinus sylvestris* treeline in the Central Swiss Alps was a product of changes in the disturbance regime altering the competitive balance, i.e. an ecological cause rather than the classic temperature hypothesis. The advent of agriculture has also added anthropogenic factors to the mechanisms regulating elevation of treelines. These are evident through livestock grazing, removal of timber to clear land for agriculture, fuel and impact on natural fire regimes. Pedological processes may also impede the advance of treelines. The elevation and structure of any individual treeline in northern Europe is a unique combination of

these factors. Factors vary in their relative importance in determining elevation, though temperature is usually considered to be the overriding factor.

1.2.3 General principles of pollen representation

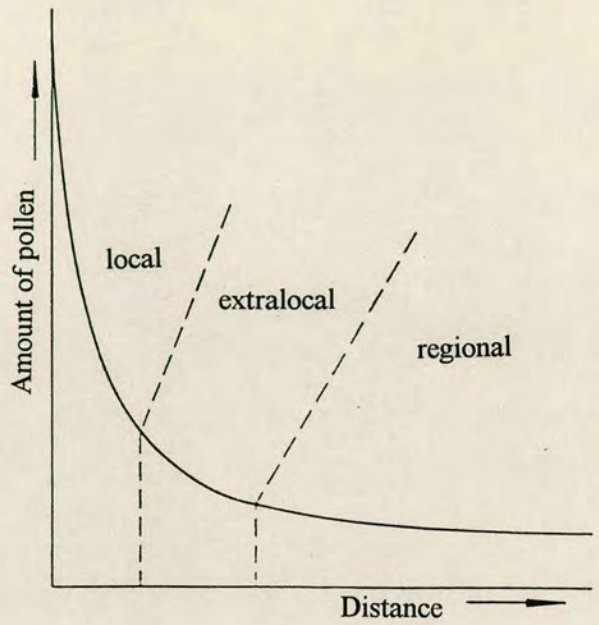
The relationships between vegetation and pollen assemblages are the basis of interpretation of pollen diagrams. Calibrating this relationship is complicated because of variations in the production, distribution and deposition of pollen (Prentice, 1985) and because of the uncertainties regarding the appropriateness of the spatial scales at which studies are conducted to the changes that one is trying to detect (Gaudreau *et al.*, 1989). These considerations are of greater importance in montane regions where the existence of steep altitudinal gradients means that vegetation belts are compressed. In particular, sampling needs to be on a finer spatial resolution. The compression of vegetation belts allows for easier study of altitudinal treelines than latitudinal treelines. The suitability of montane sites for studies on vegetation response to climate is, however, tempered by problems of determining source area where vegetation gradients are spatially short (Tallis & Switsur, 1990; Markgraf, 1980; Solomon & Silkworth 1986; Fall, 1992). This problem is exacerbated in the very steep vegetational gradients found in the Scottish mountains. Vegetation reconstruction from montane pollen assemblages is further hampered by the limitations of representation models.

Iversen (1947) was the first palynologist to document that pollen taxa could be either over, under, or equally represented in relation to vegetation abundance. He also proposed simple correction factors to account for over- and under-representation of taxa. This approach was formalised by the R-value model (Davis, 1963). The R-value model is based on the simple ratio of an individual pollen taxon in a modern assemblage to the abundance, as percentage cover, of the source species in a given radius of vegetation. The most detailed application of this model was in the calibration of forest composition and pollen rain by Andersen (1967, 1970 and 1973). The R-value model is dependent on the radius from which pollen is assumed to be derived and a taxon can vary from over-represented at one site to under-represented at another site through the fluctuations of other taxa. These are serious limitations to the application of the R-value model (Parsons & Prentice, 1981). Andersen (1970) and Bradshaw (1981) were successful in applying the R-value model under a closed forest canopy by using the y-intercept of a regression

model to estimate background pollen influx. Both these studies were in largely unforested landscapes. In a landscape with higher levels of background forest cover the resolution of moss polsters will be expected to be lower and higher y-intercepts will invalidate the use of regression models to estimate separate the regional pollen signal (Jackson & Wong, 1994). The R-value model was mathematically improved by the extended R-value model which is based on maximum likelihood estimates rather than regression estimates of the background pollen (Parsons & Prentice, 1981). While an improvement on linear regression techniques (Prentice & Webb 1986), the extended R-value model is still complicated to utilise because the background component can vary (Sugita, 1994) and because of different pollen source areas.

Questions of scale have become one of the most preoccupying issues in modern ecology (Levin, 1992). This is also true in palynology. Central to models of pollen representation is the definition of pollen source areas (Janssen, 1966; Oldfield, 1970; Birks, 1993). Using the integrated form of Sutton's (1953) equation, Prentice (1985) showed that lighter pollen types will become better represented in larger basins. This is a simplistic model, designed for homogenous forest, but does indicate that the choice of source area is critical. Widely dispersed taxa cause particular problems in this respect as they can be deposited in vegetation devoid of the producing species. This results in these taxa having infinite R-values (Parsons & Prentice, 1981). Long distance transport of pollen has been considered a 'classical source of error' in this respect (Faegri & Iverson, 1975). Incidence of infinite R-values can be reduced by increasing the radius from which vegetation estimates are made and thus increasing the probability of incorporating all species contributing to the pollen spectrum. However, selection of too large a radius will reduce the resolution needed to detect distribution patterns in less well dispersed pollen types. This differentiation between pollen production and pollen dispersal among plant species becomes much more complex when applying the models to fossil pollen assemblages. Janssen (1966) modified the R-value model to demonstrate local, extra local and regional pollen representation from modern samples. Janssen's approach is summarised in Figure 1.2.

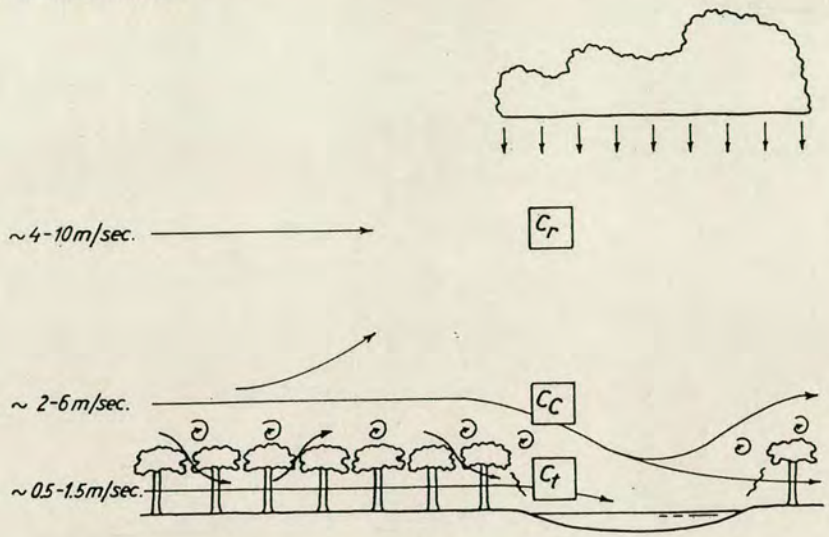
Figure 1.2: The idealised distance-decay relationship between pollen rain and distance from the pollen source, after Janssen (1966).



A rapid exponential decline in density with distance from source characterises local pollen rain. The regional pollen signal is that part of the curve which approaches a line parallel to the abscissa. Between these two extremes there is an area of transition. This is the extra-local pollen rain. Boundaries between local, extra-local and regional pollen rain are arbitrary. The contribution from each component to the pollen assemblage is dependant on many factors such as pollen dispersal, weather pattern and vegetation structure. Empirical observations suggest that small peat or lake deposits up to 50 m in diameter represent the immediate stand (Sugita, 1994; Calcote, 1995); small lakes (20-200 m) represent a 10^2-10^3 radius, larger lakes 10^3-10^4 km^2 (Bradshaw & Webb, 1985) and very large lakes 10^6 (Maher, 1977).

A pollen assemblage contains pollen deposited by different plant species with different source areas. Identification of pollen source areas is inextricably linked to mechanisms of pollen transport (Tauber, 1965). At a forest ecotone, Tauber's mechanisms for dispersal and sedimentation of pollen will apply (Figure 1.3).

Figure 1.3: Scheme showing the components of Tauber's (1965) distribution model which apply at a forest ecotone.



The trunk space component (C_t) comprises the pollen moving down from the tree canopy and up from the ground flora below the canopy. A small percentage of this pollen will be deposited outside the forest canopy by wind moving through the sub-canopy air space. Pollen from the canopy circulated above the canopy by air currents forms the canopy component (C_c). This component is the major contributor to the troposphere and therefore long distance transport (Hirst *et al.* 1967). Eddy diffusion means that most of the pollen released at a height of 20-30 m in an average turbulent atmosphere will be brought to ground within 100 m of the source (Sutton, 1953). This effect is modified somewhat as 'point sources' do not often occur in nature. Pollen sources are diffuse and the initial rise at one point may be obliterated by the effect of a down-wind source. The final applicable component is that derived from rain out (C_r). The source of pollen in the rain out component will by nature be largely regional.

1.2.4 Pollen representation at treelines

In the simplified case of pollen distribution from a forest edge Sutton's equation for particle dispersion by eddy diffusion shows that pollen concentration should be inversely proportional to the distance from the source. Modern arboreal pollen distribution from forest edges in the British Isles largely conform to this rapid exponential decline in arboreal pollen with distance from the forest edge (Turner, 1964; Tinsley & Smith, 1974;

O'Sullivan, 1973a; Cundill, 1979). A summary of the available literature for the British Isles is given in Table 1.1.

Table 1.1: Distance (m) from forest edge for a fifty percent decline in the representation of selected arboreal pollen taxa.

Author (s)	Distance
Turner, 1974 (*Pinus*)	500 m (east); 300 m (west)
Tinsley & Smith, 1974 (Transect A, mixed species)	50
(Transect B, mixed species)	20
(Transect C, mixed species)	50
Caseldine, 1981 (*Betula*)	80

However, classic models of pollen distribution from forest edges make many assumptions such as forest homogeneity, considering deposition at basin centre only, not accounting for prevalent wind direction and being susceptible to high regional pollen influxes, which may limit their use in a treeline situation. The use of Sutton's equation also needs to be reconsidered at altitudinal treelines. The smokestack form rather than the integrated form of Sutton's equation may be more appropriate at the treeline because of the change in the stature of the vegetation (*cf.* Prentice, 1985). Further, treelines may be better regarded as a plane surface rather than a point surface for pollen distribution calculations (see Strand, 1957).

Wind is also a very important aspect of the depositional environment at high altitudes. Prentice's (1985) treatment of terminal velocities of pollen at different wind speeds as a composite parameter (3 m s^{-1}) may not be applicable in the highly turbulent atmosphere at the treeline and above. Solomon & Silkworth (1986) tested the exponential decline model of pollen distribution in mountain vegetation. They found that pollen abundance changes abruptly in adjacent sites, with species in one vegetation type having most deposition locally, but having a constant rate of influx in the other vegetation types in a valley system. They described this distribution as a step function rather than a linear function and concluded from this that fossil pollen assemblages derived from distant areas would contain no information on the composition of the local vegetation. Unfortunately they did not sample above the treeline. In addition, Markgraf (1980) demonstrated that local wind

patterns have a large impact on modern pollen distribution in montane environments and that the major direction of pollen distribution is uphill, a point reiterated by Fall (1994).

Differences in pollen size and density can influence terminal velocity according to Stokes' law. These differences were utilised by Maher (1963) to interpret *Picea* treeline data in the San Juan Mountains, Colorado, where a *Pinus* forest belt occurs below the *Picea* treeline. *Pinus* pollen is one of the lightest pollen taxa with a density of 0.39 g cm^{-3} (Gregory, 1961). Maher (1963) assumed that *Pinus* was more regionally distributed and therefore deposited at a uniform rate above the *Picea* treeline. Hence, the representation of the more dense and quickly deposited *Picea* pollen in a *Picea/Pinus* ratio could indicate position of the treeline. This was achieved by using a regression of the ratio from modern samples against distance from the treeline and then using this regression to predict the 'apparent' elevation of fossil pollen spectra. If a fossil spectrum had a low ratio typical of a much higher altitude Maher concluded that at that point in time the treeline was receding. Similarly, if the ratio was typical of a lower altitude the conclusion was that the treeline had advanced. However, this approach has a serious limitation in that the *Picea/Pinus* ratio increases with altitude to just above the treeline, then decreases. Thus, separate regressions are required for above and below the treeline and the same *Picea/Pinus* ratio can indicate two different altitudes, one from above and one from below the treeline. This difficulty in determining orientation from treelines when using ratios has also been highlighted by Solomon & Silkworth (1986) and Spear (1989), but can be negated by use of indicator species. Secondly, the use of a linear regression suggests that each fossil assemblage is from a unique altitude which when plotted are oscillatory. A problem then arises in deciding which of these oscillations represent real changes in treeline elevation and which are just noise. Thirdly, the use of regression makes no allowance for intra-altitudinal variation.

1.2.5 Palynological studies at North American treelines

There has been considerable research on the latitudinal changes in arctic treelines during the Holocene (see Morisset & Payette, 1983; Spear, 1993; Lavoie & Payette, 1994 and references therein and Jacobs *et al.*, 1995). However, much less research has focused on altitudinal treelines, despite arguments for these being more sensitive to climatic change

(Davis & Botkin, 1985) and avoiding methodological problems of sampling over wide geographic areas (Gaudreau *et al.*, 1989).

Simple exponential decay models have been used to interpret treeline fluctuations with ambivalent results (e.g., Andrews *et al.*, 1975; Petersen & Mehringer, 1976). Maher's (1963) approach has been more widely used with varying results. However, temporal variations in selected pollen ratios have given conflicting indications on climatic trends and treeline elevation in the Colorado region (*cf.* Maher, 1972 and Short, 1985). Fall (1985) came to similar conclusions as Short (1985) that Holocene treelines reached their maximum extent in Colorado 7000 to 4000 BP indicating a warmer and wetter climate than today.

Further north Kearney & Luckman (1982) looked at vegetation history in the Maligne Range, Jasper National Park, Canada. Despite taxonomically poor pollen diagrams, the high variation in the pollen curves indicate dynamic vegetation changes over the post-glacial period. On the evidence of pollen, needles and some conifer stumps they suggest a lowering of treeline elevation from 1700 BP. This study was aimed at general vegetation history and not specifically at treeline fluctuations. A more analytical approach to treeline fluctuations in this region using Maher's (1963) approach gave more direct insight (Kearney & Luckman, 1983). A regression on the *Abies/Pinus* ratio was used to interpret fossil pollen spectra from two cores collected above the current treeline. As none of these spectra exceeded the maximum ratio found at the treeline only the regression model for below treeline was employed. This application indicated two periods of timberline above its current station 8500-7000 BP and 6700-5900 BP, though there was considerable variation between the two cores. The second of these periods is concurrent with the mid-Holocene optimum. From the last of these periods the treeline has oscillated around its current position. This is a result of the discontinuous nature of the regression technique and not real changes. Fluctuations in the treeline are small, with a maximum potential spread of 200 m and many movements of much less than this. MacDonald (1989) stated on the basis of a synthesis of a number of North American studies that there was broad agreement for a treeline above its modern elevation 8000 BP to 5000 BP but little clear consensus in more recent times.

1.2.6 Palynological studies at British treelines

Altitudinal treelines in Britain are composed principally of two species, *Pinus* and *Betula*, both of which are high pollen producers. However, research into the history of forest extent in the British uplands has been poor (Birks, 1988) and previous attempts to establish altitudinally constrained treelines using pollen analysis have had limited success (Maguire & Caseldine, 1985). Consequently there are very few pollen diagrams published from high altitude sites in Britain and even fewer diagrams relate to changes in elevation of the treeline. Below is a summary of those that do exist. This discussion is widened to include evidence from macrofossils in addition to pollen for the Cairngorm region.

Pollen diagrams from Cross Fell (Turner, 1984) showed that Cross Fell was wooded with *Betula* to the summit (893 m) in the past. The present treeline is 100 m below this. Turner's original hypothesis was that pollen assemblages from above the treeline should lack a local tree pollen element. In practice she found that there was little variation in the tree pollen composition at any altitude indicating that the arboreal pollen was derived from a wider area in this study. However, sites above the treeline had much higher values for the herbaceous components typical of the vegetation above the treeline and thus, the former treeline was estimated on the basis of an arboreal/non-arboreal pollen (AP/NAP) ratio. The Galloway Hills in south-west Scotland were also forested to near the summits in the past (Birks, 1970). Forests there were mostly deciduous, *Quercus*, *Ulmus* and *Betula*, with mixed *Betula* and *Pinus* forests on acidic peats. As none of these pollen diagrams are radiocarbon dated it is not possible to determine when the *Betula* treeline receded and whether the cause was climatic or anthropogenic.

Radiocarbon dated pollen diagrams, from the south Pennines, interpreted using a simple pollen influx model, clearly showed that mixed forest also reached summits over 500 m until 4700 BP (Tallis & Switsur, 1990). Decline in the altitudinal extent of the forest in the southern Pennines was synchronous with expansion of blanket peat. There is still much debate as to the cause of the expansion of blanket peat during this period at numerous sites around the British Isles (Goddard, 1970). In the southern Pennines Tallis & Switsur (1990) presented evidence for both repeated burning of upland forest by Neolithic people and climatic change. However, the model used to interpret pollen flux at the treeline in this study was based on the work of Turner (1964) and Prentice (1988), but

took no account of disruptions in the exponential decline of pollen with distance from a forest edge caused by greater turbulence at an altitudinal treeline (Solomon & Silkworth, 1986).

Porteous (1985) recorded that the *Betula* treeline at Loch Loyal in Scotland exceeded the present altitude three times in the past and was lower in the recent past. Porteous used the ratio and regression methods of Maher (1963) but, as there was no correlation between log *Betula*/Ericoid pollen and altitude for the surface samples below the treeline, precise determination of the height of higher elevation treelines in the past was not possible. It is also unclear if these fluctuations were the result of a dynamic woodland-heath interface, climatically driven treeline fluctuations or artefacts caused by recruitment processes to deposits.

Pinus treelines have also attained higher elevations in the past. *Pinus* rarely formed a major component of treelines in southern Britain where there was competition from *Quercus*, but in northern Britain *Pinus* was the major component of upland forests in the Holocene (Birks, 1988). The extension of *Pinus-Betula* forest cover during the Boreal-Atlantic transition to 770 m around Lochan nan Cat on Tayside was determined by Donner (1962) from pollen by an AP/NAP ratio. Dating the forest maximum to the Boreal-Atlantic transition is considerably weakened as it was on the basis of stratigraphy alone and these pollen diagrams were not radiocarbon dated.

The Cairngorm region has received more attention than other regions in Scotland in relation to vegetation history. Early work by Pears (1968a) describes pollen diagrams from three altitudes in the Cairngorms, all above the present treeline. These indicate that trees were not present at 917 m during the Holocene, but certainly reached 603 m. None of these pollen diagrams were radiocarbon dated and it is difficult to put precise dates on the treeline decline. For this reason it is also difficult to evoke a climate induced mechanism for recession of the treeline. Pears (1968b) advocated grazing, muirburn and timber extraction from the sixteenth to nineteenth centuries as determining the present treeline elevation. Pears postulated the natural upper limit for tree growth in the Cairngorms to lie between 600-700 m (1967, 1968) depending on wind speeds, but it is actually depressed to 500 m in most places. *Pinus sylvestris* stumps from this site show

that there was extensive forest cover up to at least 790 m, with a second layer up to 700 m (Pears, 1968a). This supported earlier descriptions of *Pinus* occurring in two distinct layers in Cairngorm peats (Lewis 1905, 1906, 1907, 1911; Samuelsson 1910). The second layer was originally interpreted as a re-advance during the Sub-Boreal (Pears, 1968a), but subsequent radiocarbon dates showed that these stumps were highly variable in age and not referable to any one period in the post-glacial (Birks, 1975; Pears, 1969, 1972, 1975a; Bridge *et al.* 1990). Selective preservation of peat stumps caused by spatial variation in local hydrology are probably the primary determinants of the distributions of preserved stumps (Pears, 1975a, 1988a).

A general relationship between 38 radiocarbon dates and altitude was found for *Pinus* stumps in the Cairngorms by Dubois & Ferguson (1985). From their data stumps of 7000 BP are the only ones to be found at the highest altitudes, i.e., 730 m, and stumps of 3000 BP and younger are not found above 530 m. However, their data were assimilated from a relatively small sampling area (approx. 8 km^2) and were based on two samples at 7000 BP or more and three samples at 3000 BP or less. The two stumps from 7000 BP predate the formation of peat deposits on this site by 1000 radiocarbon years.

The formation of peat was associated with increased levels of precipitation lasting from 6200 to 5450 BP (Dubois & Ferguson, 1985). No stumps were found above 620 m for this period, though Pears (1988a) drew attention to a stump from Meall a' Bhuachaille at 701 m which dated to 6150 BP (Pears, 1972). There was expansion of *Pinus* to higher altitudes shown using both analysis of stumps and pollen at Rannoch Moor (Bridge *et al.*, 1990) just before this at 6600 BP. With drier conditions, 5100 to 4450 BP, Dubois & Ferguson (1985) again describe stumps at 700 m plus. However, the preservation of a large number of stumps at 4000 BP is attributed to rapid peat accumulation during a second increase in precipitation. This wet period has been recorded for other parts of NW Europe (Blackford & Chambers, 1991). This was also reflected in synchronous changes across three cores indicating re-expansion of *Pinus* 4970 - 4660 BP (Bridge *et al.*, 1990).

The dearth of stumps from 3200 BP above 530 m was tentatively attributed to climate, with anthropogenic activity being rejected because of a lack of solid evidence (Dubois & Ferguson, 1985; 1988). This view was strongly challenged by Pears (1988a), who also

pointed out that a stump at 610 m on Carn Mor, dated to 2880 BP (Pears, 1969) was ignored in Dubois & Ferguson's synthesis. The climatic change at 3200 BP was not suggested by Dubois & Ferguson (1985) to be related to precipitation but rather to a drop in temperature and increased wind speeds (*sensu* Lamb, 1977). Low deuterium values, indicating heavy rainfall, were later found to coincide with 7300 BP; 6200 to 5800 BP (peat initiation and decline in treeline); 4200 to 3940 BP (bog rejuvenation and spread of blanket peats) and 3300 BP, though this last date was only represented by two samples (Dubois & Ferguson, 1988). More research effort over a wider geographic area in the Cairngorms is required to clarify which interpretation is correct.

Pinus sylvestris stump preservation is related to local hydrological conditions (Dubois & Ferguson, 1985, 1988; Pears, 1975, 1988a). Hydrological conditions can change in relation to peat development as much as to changes in regional climate, and the temporal distribution of *Pinus* stumps is a reflection of preservation which is itself conditioned by localised climatic regimes superimposed on the history of peat accumulation. Other than showing that there were *Pinus* populations present at higher altitudes than today, stumps provided little evidence of treeline fluctuations. An alternative approach to estimating treeline elevation can be taken using pollen analysis as shown by Pears (1968a).

Budworth (1984) in a previous study on the dynamics of the treeline at Creag Fhiaclach attempted to establish the elevation of previous treelines using the pollen ratio technique as outlined by Maher (1963) on a single core. The selected pollen taxa were *Pinus* and Ericoid. In constructing the regressions considerable scatter was found in ratios below the treeline and this regression was not statistically significant in direct contrast to the above treeline regression, where there was a good linear relationship with distance to 130 m above the modern treeline. Budworth recorded apparent changes in elevation varying over 266 m though it is difficult to ascertain whether these fluctuations are dynamics at the treeline rather than dynamics of the treeline.

In conclusion, all previous pollen diagrams from the British Isles show that treelines were previously at higher altitudes. However, there appears to be evidence of a broad decline in altitude around the Atlantic climatic decline, when peat expanded at higher altitudes. It is evident that the former extent of tree cover in the Cairngorms was also much higher

than in the past. *Pinus* has at least occurred above 700 m approximately 8000 years ago and again 5500 to 4400 years ago (Dubois & Ferguson, 1985, 1988; Pears, 1975a, 1988a). However, there is still a lack of precise detail on treeline history in the Cairngorms (Bennett, 1996; Birks, 1996).

2

Site details

2.1 Introduction

The Cairngorms are an ideal site for climate studies. Creag Fhiaclach (National Grid reference, NH 895055) was chosen as the site for this present study for two reasons. Firstly, it is both the highest and best example of *Pinus* treeline left in Britain (Watt & Jones, 1948; Pears, 1967; Thompson & Brown, 1992). Secondly, as the relationship between treelines and their environment is so complex, Creag Fhiaclach was an ideal choice as there has been much research conducted on the physiology and demography of trees at this site (Miller & Cummins, 1982; Wilson, *et al.*, 1987; Pears, 1988b; Grace *et al.*, 1989; Grace, 1990; Grace & Norton, 1990; James, *et al.*, 1994). Subsequently, Bunce (1996) has demonstrated that the Cairngorms are on the oceanic/continental tension zone and hence are one of the areas most sensitive to future climate change under current climatic scenarios in Europe. This is of course no indication of the sensitivity of the region in the past.

Creag Fhiaclach is part of the Inschriach Estate and is located within the Cairngorms National Nature Reserve, close to Aviemore. Past land use in the region was for summer grazing of cattle, muirburn for grouse management and extraction of timber for fuel. Today the site is grazed by red deer. The location of Creag Fhiaclach is shown in Figure 2.1 and the position of the sampling grid is shown in Figure 2.2.

2.2 Geology

The Cairngorm massif is essentially a Devonian granitic pluton encompassed by Precambrian moine schists with a drift mantel of glacial origin at lower altitudes (Harry, 1965). The topography of Creag Fhiaclach is a spur running north-south on the western flank of the massif, which has a rounded crest as a result of glacial activity. During the last glaciation ice flowed north and east along the Spey valley and till was deposited on

Figure 2.1: Map showing the location of Creag Fhiaclach (■) and Ciste Mhearad (●), in relation to Aviemore, Glen More and Rothiemurchus (modified from Pears, 1967).

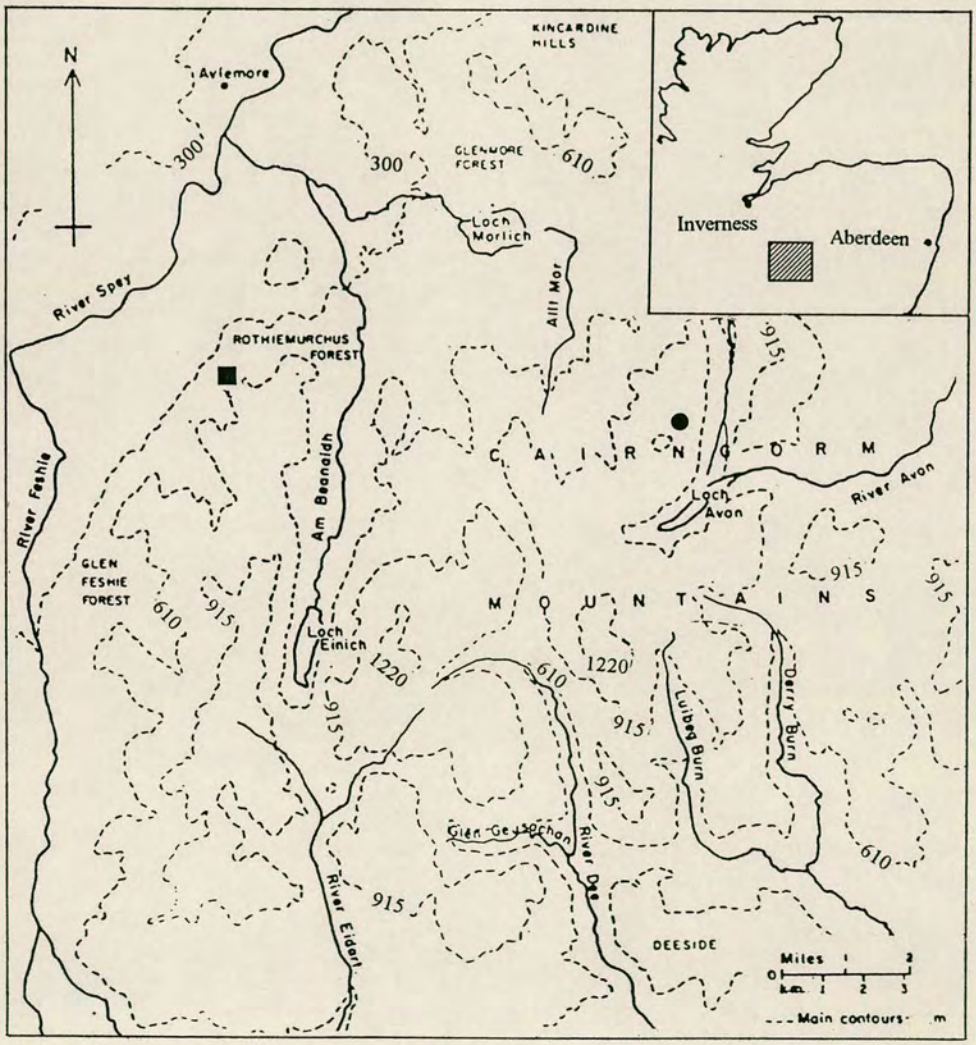
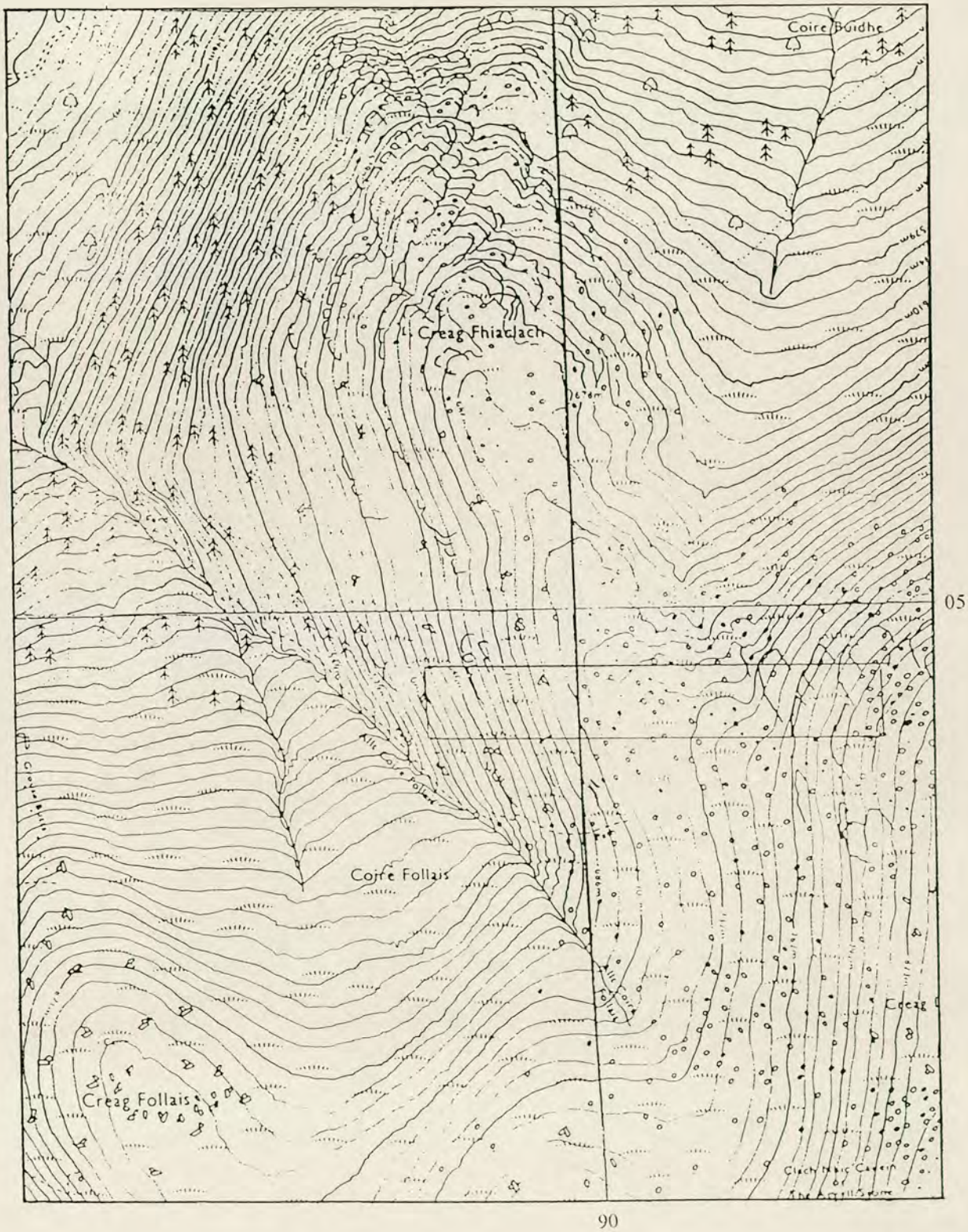


Figure 2.2: Map (1: 50,000) showing the location of the sampling grid at Creag Fhiaclach.



ground below 600 m (Sissons, 1976; Brazier *et al.*, 1996). This type of acid rock is a poor soil former, a description of the soils at Creag Fhiaclach follows.

2.3 Stratigraphy of blanket peats at Creag Fhiaclach

2.3.1 Introduction

Stratification of upland blanket peat reflects past environmental conditions. Major changes in peat stratigraphy and their relationship to prevailing climatic condition have been used as a basis for climatic sub-division of the Holocene (Blytt, 1876; Sernander, 1908). This classification has since been criticised for over simplification (Smith & Pilcher, 1973). More recently secular variations in peat deposits have been successfully used to reconstruct proxy climates (Barber, 1981a; 1982). Shifts in climatic regimes cause changes in mire hydrology which have irreversible impacts on stratigraphy.

During periods of high precipitation water tables are high reducing the rate of decomposition and increasing the length of time before the deposit enters the anaerobic zone where decomposition is slower. This produces a rapidly accumulating peat which is well preserved with a low degree of humification. Low precipitation rates reduce the level of the water table allowing oxygenation of the upper peat layers which then decompose faster producing a slowly accumulating highly humified deposit (Barber, 1981b).

The degree of decomposition is also indicative of the relative age of peat deposits. Quantifiable physical and chemical changes occur as vegetative material decomposes. Organic matter is progressively lost with time, through the release of CO_2, methane, H_2S, and other gases, or through the leaching of humic acids. Thus, relative mineral content tends to increase with depth as organic matter is lost. This increase in mineral content causes a corresponding increase in bulk density. Bulk density is also increased by compaction with depth. Compaction reduces pore space and hence water retention capacity. The simplification and reduction in the size of large organic structures with depth further aids compaction.

The extent to which all these processes have occurred in the upland blanket peat at Creag Fhiaclach was determined by standard stratigraphic tests. The aim was to identify and

differentiate stratigraphic markers to enable pollen spectra from different cores to be compared.

2.3.2 Sampling

Two types of material were sampled from Creag Fhiaclach, moss polsters and peat cores. All the moss polster samples were 5 cm x 5 cm and were composed mostly of *Hylocomium splendens*. The peat cores were 4 cm x 4 cm with varying depth. These samples were collected from a sampling grid as set out in Figure 2.3. The grid consists of nine altitudinal axes, 100 m apart, parallel to the contour. The two lower axes are within the *Pinus* forest, the third is across the treeline and the remaining six are above the treeline. The latitudinal axes are 30 m apart and the number changes from four at the three highest altitudes to five at the six lowest altitudes.

Four replicate moss polsters were collected from all nine altitudes and are represented in Figure 2.3 as circles (B9-E1). Subsequently, five replicate peat cores were collected from the six lowest altitudes (A6-E1). Four of these replicates overlap with sampling points for the moss polsters and are represented as filled circles (B6-E1), with the fifth replicate collected from the north side of the grid. The additional replicated peat cores (A6-A1) are represented by unfilled boxes.

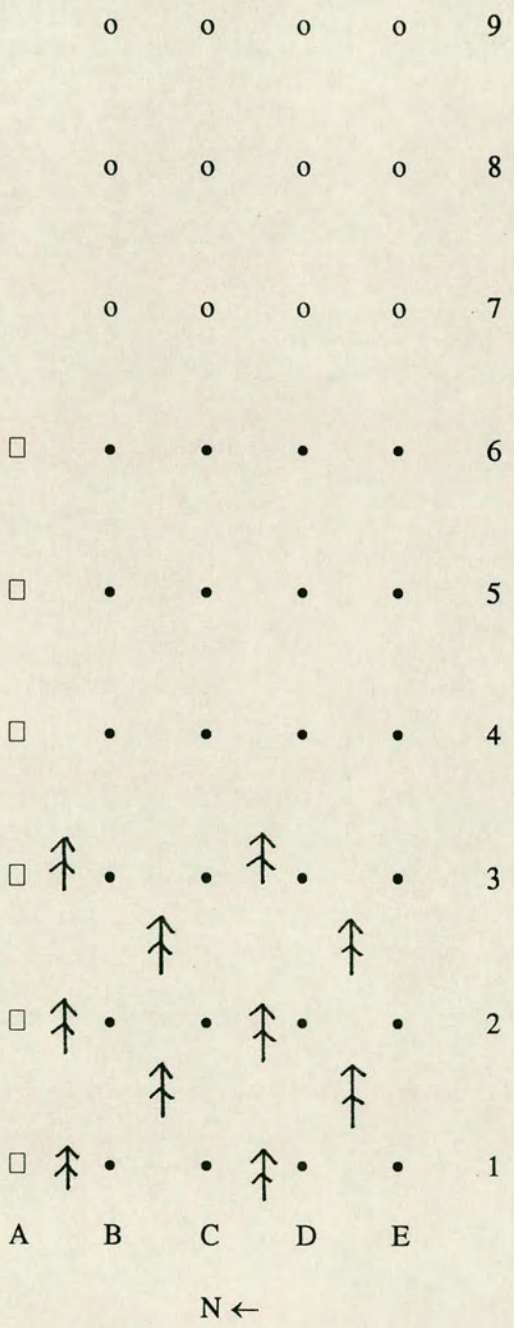
2.3.4 Methods

The measurement and description of the peat deposit at Creag Fhiaclach is based on the cores sampled from the six lowest altitudes (Figure 2.3). Visual characteristics were recorded for all thirty cores; physical characteristics and humic acid content where determined from contiguous 0.5 cm samples from one core chosen randomly from each altitude. The methods, results and description of the peat deposit from these cores forms the remainder of this chapter.

Visual characteristics

One of the first systems for peat classification was a ten-class humification (H) scale where peat was assigned to a class on the basis of colour, texture, moisture content, and the structure of *Sphagnum* macrofossils (von Post & Granlund, 1926). Tröels-Smith (1955) produced a similar classification with five classes. Both of these classifications have

Figure 2.3; Schematic diagram showing the relative positions of the moss polsters and peat cores sampled from Creag Fhiaclach. Those points on the grid sampled for moss polsters only are indicated by o, those for peat cores only by □ and those points sampled for both moss polsters and peat cores are indicated by •.



several limitations when applied to a well humidified and compressed upland peat. Firstly, the characters used to classify the peat types do not vary sufficiently to differentiate the profile into useful sections. Secondly, these classifications are subjective. Thirdly, *Sphagnum* macrofossils are not common in upland blanket peats and were only present in a single core from Creag Fhiaclach. To overcome these deficiencies additional visual characteristics were also recorded. These had the advantage of being more objective and being measured on a continuous scale providing more resolution for detection of changes in the peat profile. Recording of visible characteristics on all cores followed Hodgson (1978), Table 2.1.

Soil colours were measured by comparison with Munsell colour charts (1954). This system identifies colour in terms of three attributes; hue, value and chroma. Hue indicates the relation of a colour to red, yellow, green, blue and purple. Value describes the degree of lightness/darkness of a colour in relation to a neutral grey. Chroma is the strength of a colour in relation to a neutral of the same lightness. Both colour names and Munsell Colour Notation were recorded for a freshly broken surface for each sample. Changing light conditions and effects of oxidation may have influenced these results.

Table 2.1: Soil characteristics recorded for the upland peat at Creag Fhiaclach.

Characteristic	Classes	Description
Horizon notation	as per Hodgson	
Horizon thickness (cm)		
Horizon boundaries		
Distinctness of boundaries	sharp	- change to next horizon occurs within a < 0.5 cm zone
	abrupt	- 0.5 - 2.5 cm thick
Form of boundary	smooth	- plane surface, no irregularities, same depth across profile
	wavy	- with broad, shallow regular pockets
	irregular	- pockets deeper than they are wide
	broken	- boundary is discontinuous
Roots diameter size classes	very fine	- < 1 mm
	fine	- 1-2 mm
	medium	- 2-5 mm
Lithology of stone components		
Wet colour	see below	

Physical characteristics

Bulk density reflects the physical structure of the peat matrix. If pore spaces are large, bulk density is low and *vice versa*. Compaction of the peat can also be measured by bulk density. The degree of compaction in conjunction with a few radioisotope markers allows peat accumulation rates to be estimated. To ensure that changes in bulk density were not caused by the presence of granite in the deposit the loss-on-ignition was also determined.

Peat samples of 3 cm^3 were weighed and placed in an oven at 105 ^{o}C and dried to constant weight. After re-weighing, 0.1 g of the sample was kept aside for humic acid extraction. The remainder of the sample was transferred to a muffle furnace at 430 ^{o}C for 16 hours. Loss-on-ignition at 430 ^{o}C gives an accurate, simple and quick method of assessing organic content in soils. Temperatures higher than this may cause CO_2 loss from elemental carbon (Davies, 1974). Elemental carbon may be present if the forest has been burned in the past. Bulk density was calculated as a dry weight cm^{-3}.

Extractable humic acids

The degree of chemical decomposition of the organic component was determined by the quantity of extractable humic acids. This method provides a semi-quantitative method for determining humification by calorimetric measurement of acids extracted with sodium hydroxide. The method followed Aaby (1986) which was critically reviewed by Dugmore (1987). A sample of 0.1 g oven-dried peat was ground using a pestle and mortar and placed in a 100 cm^3 conical flask. To this 50 cm^3 of 5% NaOH was added and the suspension was simmered on a hot plate for one hour. The content of the flask was then made up to 100 cm^3 with distilled water and the suspension filtered. A 50 cm^3 aliquot of the filtrate was made up to 100 cm^3 and light transmission at 540 nm was recorded in a colorimeter. Percentage light transmission decreases with higher degrees of humification. Measurement of transmission was done as quickly as possible as the solution fades with time. Where percentage light transmission was below 20% the extract was diluted 1:2 and transmission remeasured. Transmissions were corrected for the inorganic fraction in the peat as mineral material in the peat can physically displace organic matter and cause a linear increase in light transmission (Dugmore, 1987).

2.3.4 Results

2.3.5 Visual characteristics

Profile development was poor in all cores. Other than a few centimetres of fresh litter at the top of each profile, the remainder of all profiles were von Post class 9-10 and Tröels-Smith class 5 - well humidified peat. All thirty cores had a litter (L) horizon and a well decomposed, amorphic peat (H) horizon. In addition six cores had a partly decomposed litter (F_1) horizon and a further six had a mineral-rich humified peat (Bh) horizon. Horizon depths are shown in Table 2.2.

Table 2.2: Mean and standard deviations (SD) of horizon depths in peat cores from all altitudes at Creag Fhiaclach (n=30).

Horizon	Mean depth (cm)	SD
L - litter	1.9	2.2
F_1 - partly decomposed litter	9.4	12.5
H - amorphic peat	10.5	4.7
Bh - mineral rich peat	7.5	8.7

There was considerable variation in the depth of horizons with many cores having one or more horizons absent or only slightly represented. The litter horizon was generally the shallowest though one sample had 8 cm of litter. The remaining three horizons, if present, were usually well represented. All horizon boundaries were sharp and smooth. Colour varied considerably in the litter horizon and was nearly impossible to measure. Where the litter was of sufficiently uniform colour to measure it was generally dark reddish brown (5YR 3/2 - 3/3). The F_1 horizon was quite variable in colour from dark reddish brown (5YR 3/3) to very dark brown (10YR 2/2). Both the H and Bh horizons were consistently very dark brown (10YR 2/2) or black (7.5YR 2/0). Very fine to fine roots were abundant in the F_1 and H horizons. Roots became less abundant in the Bh horizon. A few medium roots were found in the H horizon. No coarse roots occurred in any of the cores. The distribution of granite particles was generally towards the bottom of the cores. Occasionally thin layers of granite were observable in other horizons. These layers were shown to be horizontal by x-radiography (see Chapter 7).

2.3.6 Physical characteristics

Bulk density

Bulk density results are presented as plots against depth (Figure 2.4). There was a trend to increased bulk density with depth at all altitudes except at 758 m. Variation in bulk density with depth has a cyclic component at all depths except 717 m and 707 m, but there was no synchrony in these cycles. The cyclic pattern will have contributed to the low R^2 values on the linear regression of bulk densities with depth, though the regressions were statistically significant ($p < 0.05$) at all altitudes except 758 m.

Loss-on-ignition

The three lowest altitudes all had loss-on-ignition values consistently over 80% (Figure 2.5). Only one value fell below this at 707 m. At the two highest altitudes the litter layers were virtually 100% organic matter. The top few centimetres of the humified peat were also high in organic matter. However, at lower depths the amount of organic matter was variable because of the erratic presence of small grains of granite. Regressions between loss-on-ignition and depth were weak (Figure 2.5). Despite this the linear regressions were significant ($p < 0.01$) at four altitudes. Only at 707 m and 606 m were the regressions non-significant. The overall trend in loss-on-ignition indicated a decrease in organic matter content with depth.

Moisture content

Values for moisture content were up to 400% of dry weight, except at 758 m where values reached 1000%. The R^2 values for moisture content were again very low (Figure 2.6). The cores were stored horizontally at 4 ^{o}C for up to a month before the stratigraphic measurements were made and this may have allowed the moisture content to become more uniform, obscuring any trend with depth. However, the regression of moisture on depth was significant at all altitudes except 707 m and 606 m but, there was no consistent trend in moisture content: some cores had moisture contents decreasing with depth and some increasing.

Figure 2.4: Changes in bulk density down profiles from different altitudes at Creag Fhiaclach. Samples were collected in May 1992. The regression r^2 is shown for each altitude, along with statistical significance (NS = non-significant, * $P<0.05$, ** $P<0.01$, *** $P<0.001$).

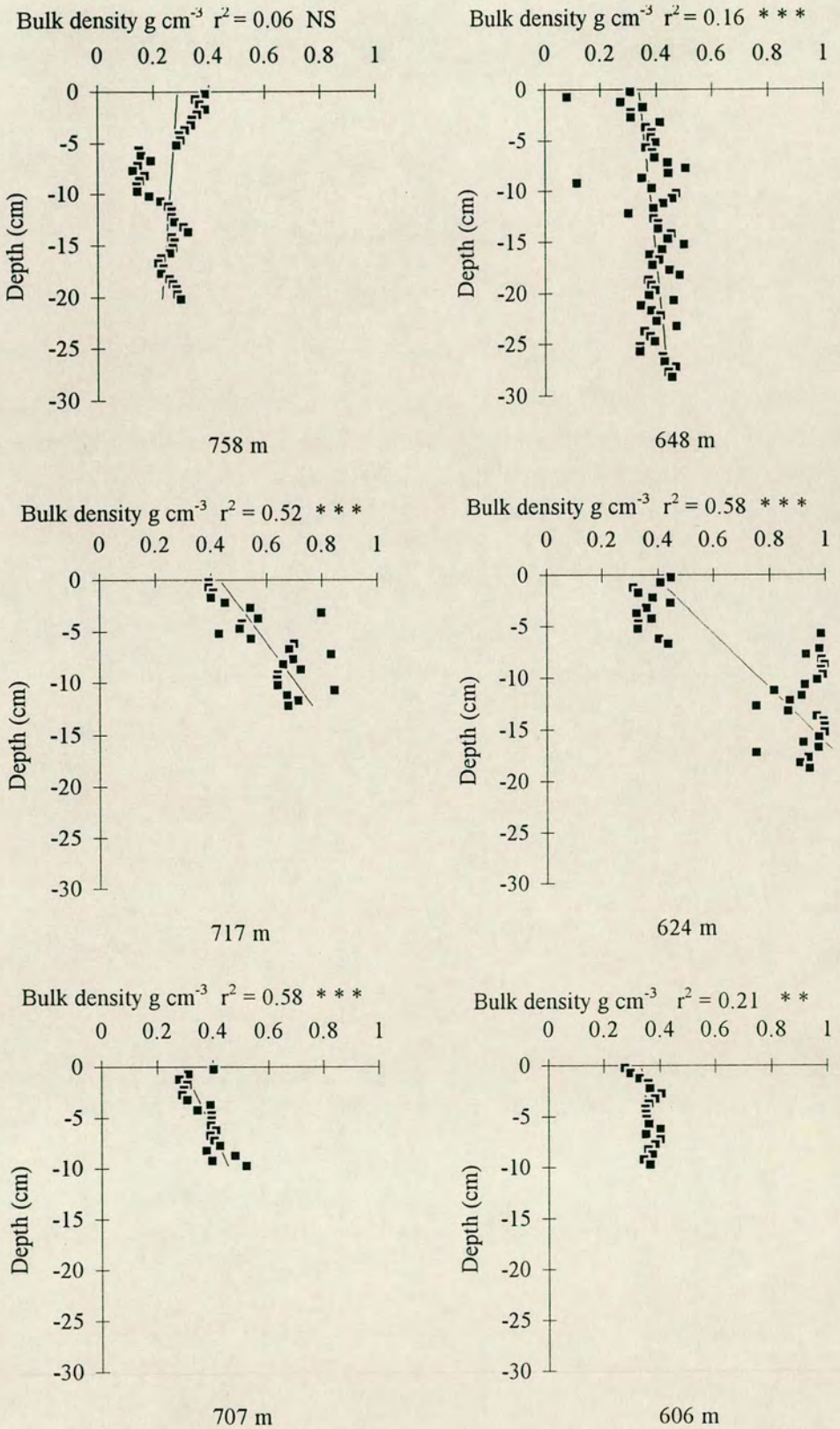


Figure 2.5: Loss-on-ignition curves at 430°C down profiles from different altitudes at Creag Fhiaclach. Samples were collected in May 1992. The regression r^2 is shown for each altitude, along with statistical significance (NS = non-significant, * $P<0.05$, ** $P<0.01$, *** $P<0.001$).

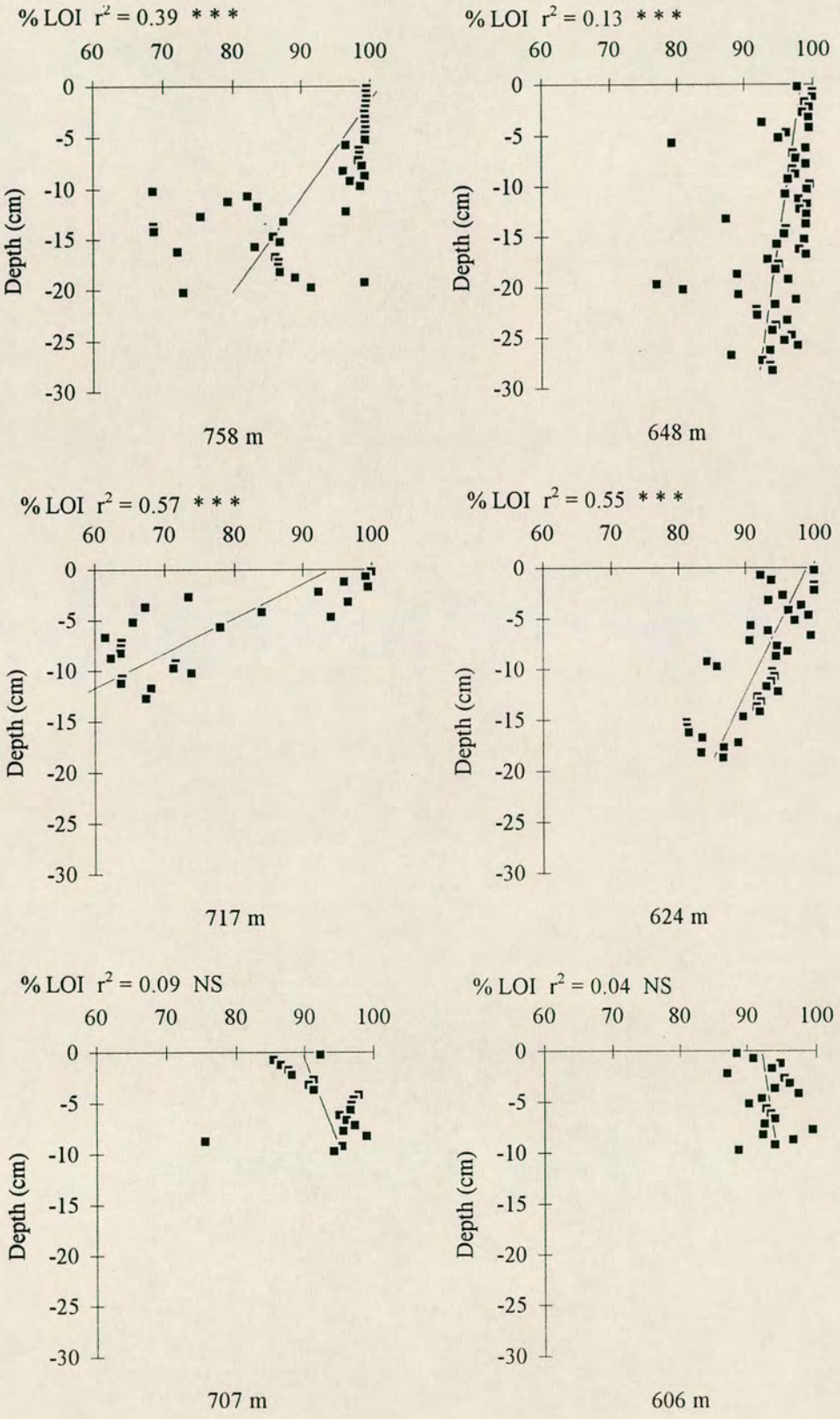
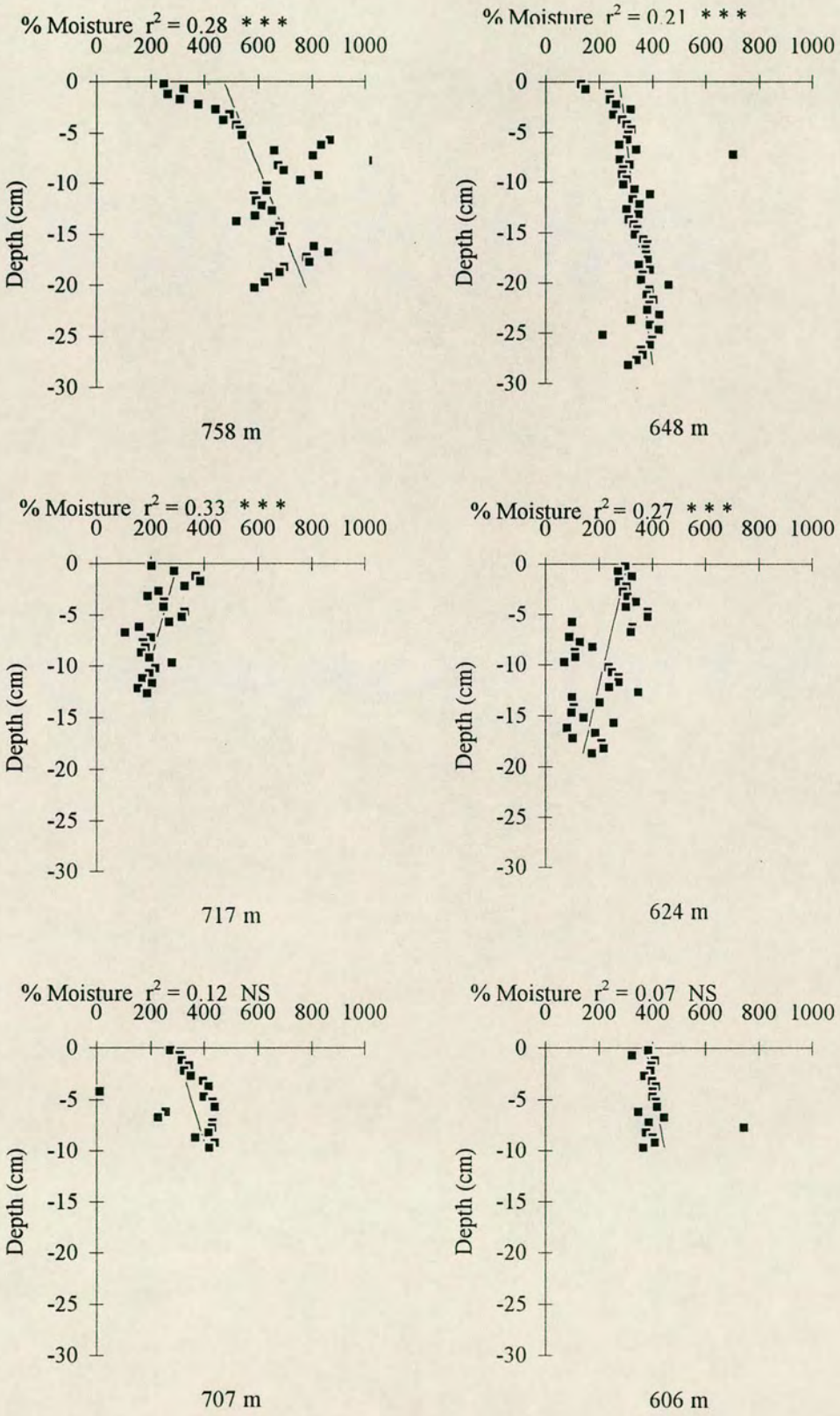


Figure 2.6: Variation in moisture content down profiles from different altitudes at Creag Fhiaclach. Samples were collected in May 1992. The regression r^2 is shown for each altitude, along with statistical significance (NS = non-significant, * $P<0.05$, ** $P<0.01$, *** $P<0.001$).



Extractable humic acids

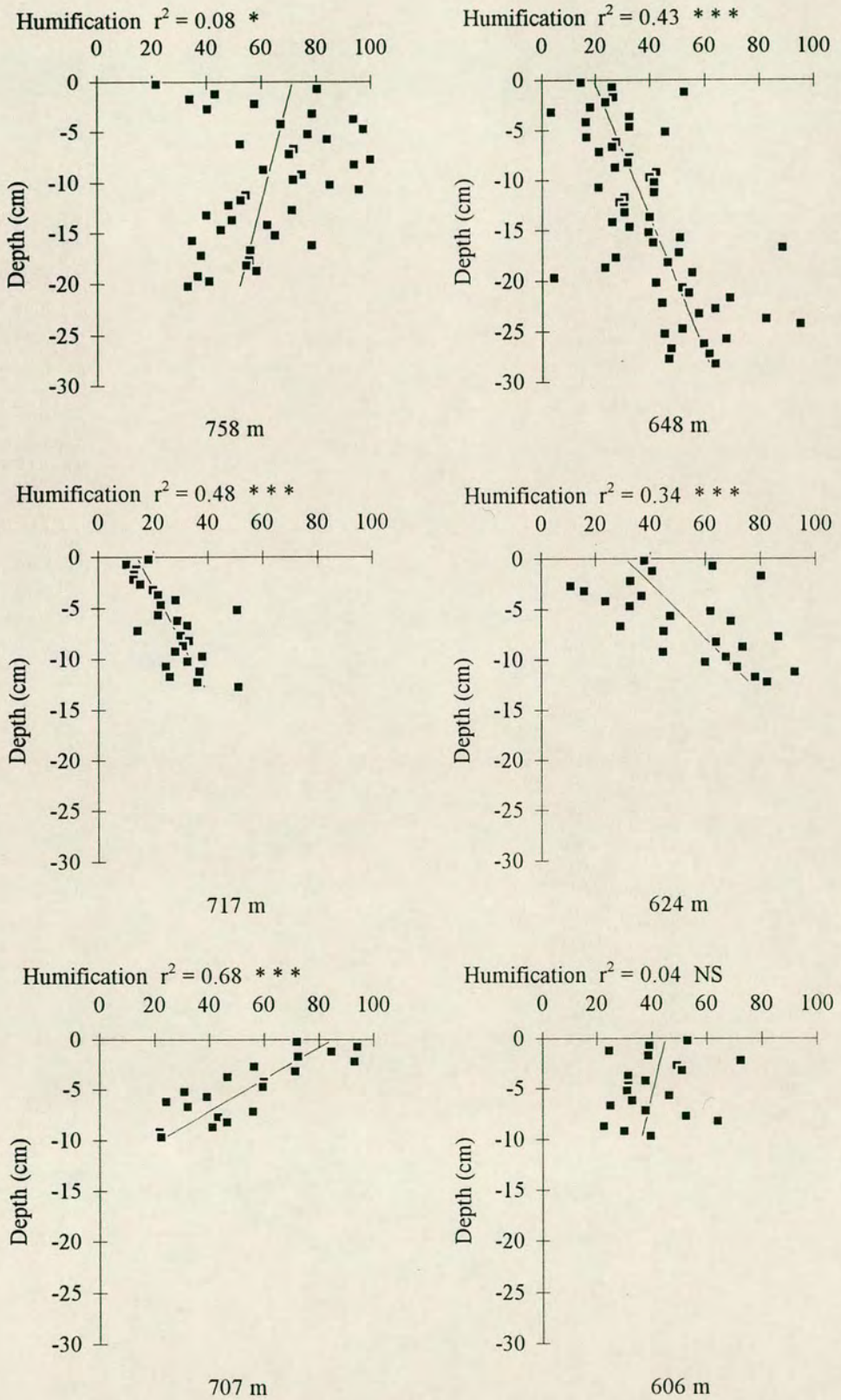
Changes in humification, with depth gave conflicting results. There was greater humification near the surface at 758 m, 707 m and 606 m (Figure 2.7). Of these only the regression line at 707 m was significant ($p < 0.01$). The remaining altitudes, 717, 648 and 624 m had negative correlations with depth with low R^2 values, though all three regression lines were significant ($p < 0.01$).

2.3.7 Discussion

Peats at Creag Fhiaclach had little structure or differentiation. The classification systems of von Post & Granlund (1926) and Tröels-Smith (1955) do not have the resolution to detect subtle changes in upland peat stratigraphy. Measurement of specific visual characteristics on a continuous scale only revealed one boundary which was common to all thirty cores, the bottom of the litter layer. This boundary was used later in the palynological study. The physical characteristics showed some general trends but none was strongly correlated with depth. Moisture content was especially conflicting. This may have simply been an effect of storage, though Levesque *et al.* (1980) demonstrated that water holding capacity was not always correlated with decomposition and thus depth.

Bulk density increased generally with depth in concordance with a general decrease in loss-on-ignition. Though the regressions were weak, the trends were consistent with increasing mineral content as organic matter was lost. In upland systems mineral material can be added to the peat by weathering of exposed rock uphill followed by wind or water deposition; in-washing from eroding peat uphill; or as tephra deposition from volcanic eruptions. Where these processes have occurred they tend to form discrete bands in the peat profile (see Chapter 7). This type of event would explain some of the cyclic patterns seen in the bulk density plots, though parallel patterns in the loss-on-ignition results were not observed. Mineral content can have non-linear effects on humification measurements (Schnitzer & Skinner, 1967). Clay particles can bind to the extractable humic acids and reduce their solubility in alkali. However, the mineral material in the cores from Creag Fhiaclach was of larger particle sizes than clay.

Figure 2.7: Changes in humification, as measured by extractable humic, acids down profiles from different altitudes at Creag Fhiaclach. Samples were collected in May 1992. The regression r^2 is shown for each altitude, along with statistical significance (NS = non-significant, * $P<0.05$, ** $P<0.01$, *** $P<0.001$).



Analysis of the stratigraphic characters measured from Creag Fhiaclach blanket peats and depth in the deposit revealed some general patterns but no consistent linear relationships. Several factors will have contributed to this. Firstly, as stratigraphic characters were only measured from one core at each altitude sampling errors will be large. However, it is the variation with depth and not altitude which is of interest here. Preliminary results from the stratigraphic tests indicated that a strong stratigraphic correlation was unlikely to be obtained and therefore analysis of further cores from each altitude would have been unjustified. Secondly, the question of sampling resolution is always a difficult one (Green, 1983). Sampling at 5 mm intervals was chosen on the basis of tephra deposits in lowland raised bogs (Valerie Hall, pers. comm.). Finally, local hydrological patterns (Aaby & Tauber, 1975) and variation in botanical composition (Clymo, 1978), which are extremely difficult to take into account, will influence decomposition processes and thus the stratigraphic variables measured here.

2.3.8 Conclusions

Visual stratigraphy appears to be slightly more useful than the standard stratigraphic tests employed. This could be a function of the larger number of samples used to derive the visual data. However, the only consistent visual marker was the bottom of the litter horizon. This was used in the subsequent palynological investigation.

2.4 Regional Climate

The Cairngorms formed a local ice centre during the Pleistocene glacial events. Mean January and July temperatures at sea level in the 1,000-1,500 years following the Loch Lomond Stadial (11,200 BP) have been estimated at -12 °C and 6 °C respectively (Price, 1983). This estimate has been challenged by Dubois & Ferguson (1985) on the presence of *Myriophyllum alterniflorum* pollen in the pollen record and a mean July temperature of 10-12 °C at low elevations. Calculations, based on Milankovitch theory, estimate an 8% increase in summer solar radiation and a corresponding decrease in winter insolation between 10,000 and 8,000 BP in the northern hemisphere heralding the present post-glacial (Birks, 1988). From this time to the present day colder, wetter periods have occurred at 7300 BP (start of the Atlantic period); 6200-5800 BP; 4200-3940 BP; and 3300 BP (Dubois & Ferguson, 1985, 1988). Data in relation to specific warm periods are harder to find for the Cairngorm region.

The climate is fairly continental, being 96 km from the sea at the closest point. Temperatures are cool with a mean July temperature of 15.1 °C and a mean January temperature of 4 °C and annual precipitation is 820 mm at 250 m (James *et al.* 1994). However, ecological gradients on British mountains can be particularly steep (Pears, 1968c; Barry, 1992) and lapse rates in the British uplands are notoriously variable (Grant & Hunter, 1962). Lapse rates for Creag Fhiaclach are very high at -9 °C km^{-1} in the 450-850 m zone (Wilson *et al.*, 1987), though these concord with rates of -6 to -10 °C given by Harding (1978). This will give mean July and January temperatures of 11.5 °C and 0.4 °C, respectively, at 650 m. Altitudinal increase in wind speeds given by McClatchey (1996) are 6-9 m s^{-1} km^{-1} rising to nearly 10 m s^{-1} km^{-1} in winter. However, wind speeds at lower altitudes (up to 663 m) can be considerably slower at 1.6 m s^{-1} km^{-1}. The average annual wind speed at the summit of Cairn Gorm is 13 m s^{-1} though annual wind speeds will be lower at lower altitudes. As winds circulate around large topographical features and the predominant wind direction is westerly, local winds will be perpendicular to the spur at Creag Fhiaclach creating strong anabatic air movements.

2.5 Holocene vegetation history in the Cairngorm region

Development of vegetation in the Cairngorm region began immediately after the ice retreated about 11,200 BP. Shortly after this, ice recovered the higher altitudes and vegetation succession was arrested until 10,000 BP when the ice finally retreated completely. The composition and structure of the late-glacial vegetation and Holocene forests of the region have recently been reviewed by Bennett (1996) and thus only a very brief account is given here. Early sucessional vegetation in the region consisted of sparse Gramineae and Cyperaceae communities on freshly exposed glacial till material (Birks & Mathews, 1978). Shrub communities with arctic characteristics developed, dominated in the early stages by *Betula nana* and *Empetrum* and later by *Juniperus communis*. As early soils developed the vegetation, enriched in herbaceous elements and shrubs, declined in favour of a more diverse forb vegetation (Birks & Mathews, 1978; Huntley, 1994). One of the commonest taxa in the pollen assemblages of this time was the *Artemisia*-type (Tipping, 1985). *Artemisia* cannot be identified beyond generic level and *Artemisia* species generally produce large quantities of pollen so the contribution of *Artemisia* to the vegetation is difficult to determine. The closest comparable type of *Artemisia* community only exists in drier regions of the Russian arctic today and the composition and ecology of

the *Artemisia* community of the eastern Scottish Highlands during the late-glacial remains elusive. This open herbaceous community was colonised by *Betula* species and slightly later by *Corylus* as the climate continued to ameliorate (Birks & Mathews, 1978). The early Holocene forests in the Cairngorm region were dominated by *Betula*, a common dominant in early Holocene forests (Vasari, 1977) with elements of other deciduous trees such as *Corylus*, *Quercus* and *Ulmus* in the flora (Birks, 1970, 1975; Birks & Mathews, 1978).

Pinus has been an important element in the flora of the Cairngorm region since the early Holocene. There was a rapid *Pinus* expansion between 7500 and 4000 BP with a decline lasting 100-200 yrs post 4000 BP (Bennett, 1984). Widescale shift in agriculture to a pastoral system meant that many forest areas were cleared from 4000-3000 years ago (O'Sullivan 1974, 1975). It is difficult to determine the scale of these clearances within the region from the pollen record (Bennett, 1996). This resulted in an overall decline in arboreal pollen with concurrent increases in the representation of *Calluna*, Gramineae and other herbaceous pollen types. Some pollen diagrams show slight increases in the arboreal pollen curves in the very recent past as a result of reforestation in the region (Birks, 1970). Today the forests are dominated by *Pinus* and *Betula* though *Betula* is less common in the southern Grampians (Durno, 1957).

2.6 Present vegetation

Gleann Einich below Creag Fhiaclach has a typical assortment of *Calluna* heath, *Betula/Pinus* woodland and plantations of *Pinus*, *Picea sitchensis* and *Pseudotsuga menziesii*; vegetation types found throughout the Grampian region. The lower slopes of Creag Fhiaclach itself comprise pinewood-*Vaccinium*-moss association (Figure 2.8) as defined by McVean & Ratcliff (1962) which are relicts of the Caledonian pinewood previously of much greater extent in Strathspey (Steven & Carslisle, 1959). Isolation, topography and 'leggy' *Calluna* growth below the current, artificial lower treeline have meant Creag Fhiaclach has been left relatively intact from the forest clearances episodes (Dickson, 1993).

The vegetation composition along an altitudinal gradient was recorded from Creag Fhiaclach in the summer of 1993. Species abundance was recorded in five replicate

quadrats centred on the moss polster sample (see Chapter 4), with intermediate altitudes sampled at the treeline. Quadrats were 10 m x 10 m to 648 m and 4 m x 4 m at altitudes above this. Data from the survey are summarised in synoptic tables given in Appendix I.

The forest consisted of a relatively uniform stand of *Pinus sylvestris* of good form. The understorey was mostly *Vaccinium* spp. over a persistent carpet of hypnoid bryophytes. The treeline itself is a sharp transition from trees to heath. While the density of trees does not decline significantly with altitude (Miller & Cummins, 1982), the stature of the trees does. The treeline on this site was composed of a narrow band of krummholtz individuals (Figure 2.9), as defined by Griggs (1946), with a few isolated trees above the treeline of good form (Figure 2.10). The age structure of the stand was uniform (Grace & Norton, 1990) with little regeneration.

The forest ecotone at Creag Fhiaclach differs from the classic treeline ecotone described by Crawford, (1989). The classic ecotone has a closed forest limit with a krummholtz zone above it. Throughout the krummholtz zone are scattered isolated trees, the upper limit of isolated trees is referred to as the tree limit. At Creag Fhiaclach there is the limit of closed forest followed by a narrow ecotone of krummholtz trees above which there are very few isolated trees. *Pinus* occurs above the treeline as numerous saplings which decrease in frequency with increasing altitude (Miller & Cummins, 1982). Stunted *Pinus* saplings occur to just beneath the top of the spur at the Argyll Stone, the demographic distribution of these is given in Millar & Cummins (1982). The treeline, however, is not a straight line but a sinuous line where pockets of heath and forest interdigitate.

Around the treeline is a diffuse band of *Juniperus communis* forming a small scale mosaic of *Juniperus communis*, *Calluna* and *Pinus*. Amongst and under the *Calluna* is a dense mosaic of *Vaccinium myrtillus*, *Vaccinium vitis-idea* and *Empetrum nigrum*. Above the immediate treeline vegetation, dwarf *Calluna* is dominant but *Juniperus* and krummholtz *Pinus* with a few isolated trees of good form still occur. While the cover of *Calluna* does not change significantly with altitude above the treeline, there is a reduction in height of the plants (Table 2.3).

Figure 2.8: *Pinus sylvestris* stand on Creag Fhiaclach at approximately 600 m a.s.l. The trees are of good form and the underlying block scree is just visible in the foreground.

Figure 2.9: Structure of the vegetation at the treeline, showing the mosaic of krummholtz *Pinus*, *Calluna* and *Juniperus communis*.

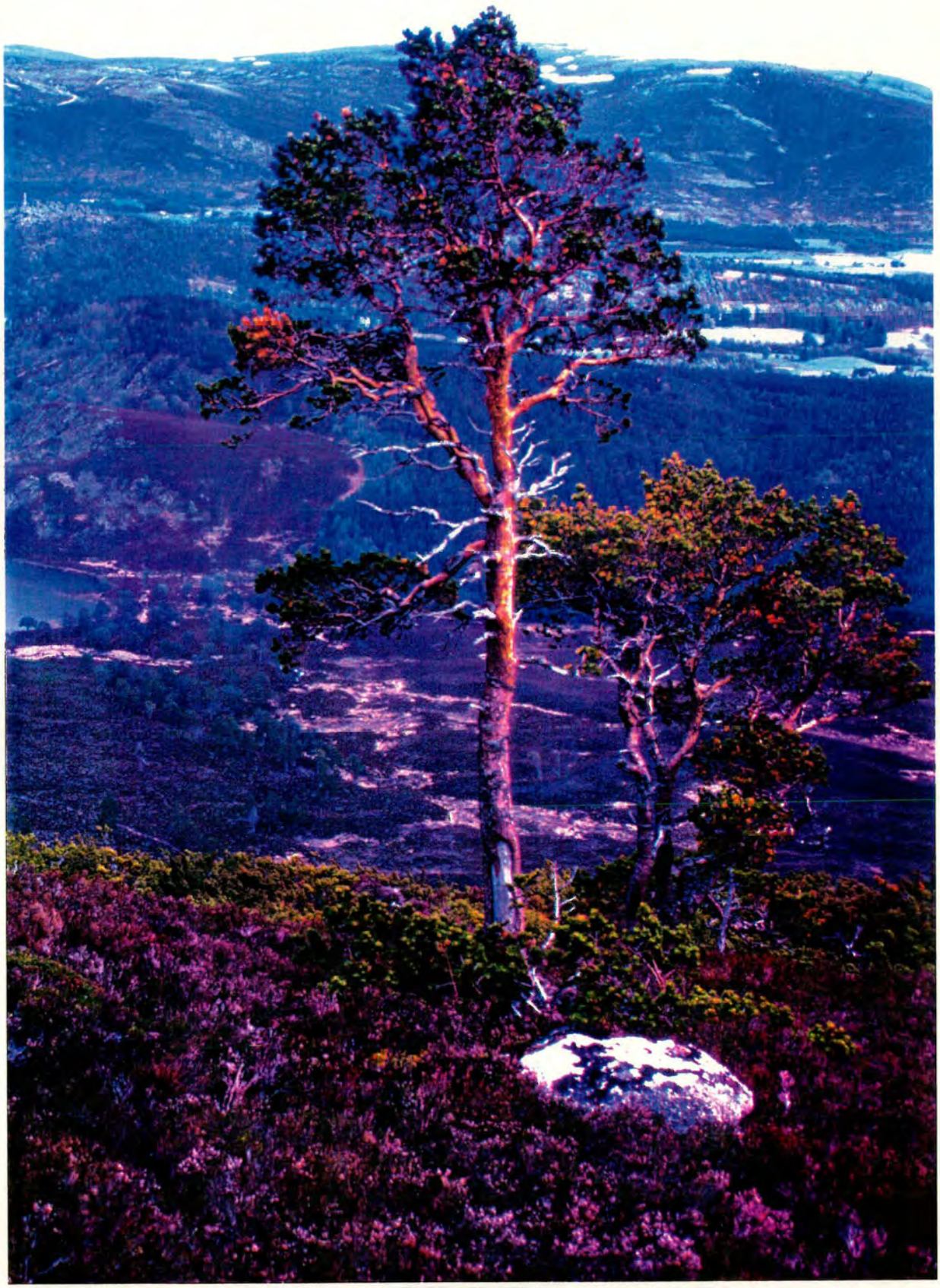


Figure 2.10: Isolated *Pinus* tree 25 m above the treeline at Creag Fhiaclach. *Calluna* in the foreground is flowering heavily.

Table 2.3: Changes in the height of *Calluna vulgaris* with altitude at Creag Fhiaclach. *Calluna* was shortest in the forest, tallest at the treeline and shows a trend of declining stature with elevation above the treeline. Measurements are given in cm with standard deviations.

Altitude	Mean (n=5)	SD
606	15	5.6
624	6	2.6
636	16	12.3
648	41	27.8
678	24	5.9
707	23	10.0
717	17	10.0
758	15	10.9

At altitudes above those included in this survey, *Calluna* height becomes further reduced and there are more frequent patches of *Juncus trifidus*. Bare ground also becomes much more frequent. This pattern of zonation at Creag Fhiaclach fits into the broader pattern of the region. (Watt & Jones, 1948; Burnett, 1964).

3

Methods and Procedures

3.1 Introduction

The gross stratigraphy at Creag Fhiaclach is of a thin layer of blanket peat over block scree, and macrofossils do not occur above the current treeline. Previous treelines were therefore, investigated at this site using palynological analysis. This chapter begins with a brief introduction to the palynological method and its limitations, followed by a description of the project design. The remainder of the chapter consists of an outline of the laboratory procedures followed during pollen preparation in Chapters 4 - 6 and the data-handling routines used in Chapter 5.

3.2 The palynological method

Pollen, spores and other palynomorphs are distinct, abundant and well preserved under anaerobic conditions. Palynomorphs are preserved in a stratigraphical sequence in peat deposits and lake muds, with the sediment forming a palimpsest. If a core of sediment is extracted and pollen concentrated from a defined depth, in combination with techniques for dating sediments, the previous vegetation at the site can be reconstructed. As species distributions are coupled to climatic conditions the fossil pollen assemblages can be calibrated against modern pollen assemblages from known climate regimes and previous climate regimes can thus also be reconstructed from the pollen record. In this manner a history of climate change and the vectors of change can be built up. This approach is now widely used in predictive modelling of climate change (Overpeck *et al.*, 1991).

However, there are many assumptions and sources of error associated with each stage in the reconstruction process. Palynology is of necessity largely restricted to wind pollinated plants. This has two implications. Firstly, insect pollinated or apomictic species will be under-represented in the pollen record. Secondly, the pollen of wind pollinated plants is adapted for wide dispersal. Therefore, pollen deposition at a particular locus can have

originated from a wide source area. Establishing the pollen source area is one of the fundamental complexities of palynology (Oldfield, 1970; Prentice, 1985; Chapter One). In addition, wind pollinated plants which are under stress may not flower. This will tend to occur more frequently at geographical or ecological range boundaries. There may also be periodic fluctuations in pollen production. This can vary from annual fluctuation to variation over several decades, perhaps as a result of slight climatic downturn.

Once the pollen has been deposited there are several factors which can affect its inclusion in the sediment. The surface of deposits, even peat deposits at high altitudes, are not static entities. Bioturbation in peats and sediment focusing in lakes causes disruption of recent pollen records. This effect is reduced with depth as layers become compressed and variations over time become dampened. After incorporation in the sediment there are problems of preservation associated with hydrological processes in the peat. Periodic aeration and water logging lead to erosion of first the intine and then the exine. This source of error falls off quickly down the profile until the permanent anaerobic zone is reached. There decay will continue but at much slower rates. Some pollen taxa are much more prone to decay than others and this differential preservation can cause problems in interpretation.

Preparation of pollen from sediments prior to counting will also have errors associated with each procedural stage. The source and extent of error will depend on the type of sediment and analytical process used. Once prepared for counting there are also problems of resolution of identification. Some plant species produce very distinct pollen, in other cases pollen taxa can only be identified as far as genus and with families such as Gramineae, other than some size distinctions (Andersen, 1979) there is no finer resolution. Obviously the coarser the resolution the lesser the ecological information which can be extracted from the data. Choice of pollen sum can also be critical if real changes are to be separated from apparent ones and presentation of pollen data also needs consideration. Expressing the data as percentages has intrinsic pitfalls. If the abundance of one taxon suddenly increases the relative proportions of the other taxa to the pollen sum will decrease. Absolute pollen methods counteract this (Peck, 1974) with the commonest method being the use of exotic markers (Mahers, 1981). However, this is not a panacea. Distortion of profiles due to uneven compaction and/or uneven rates of sediment

accumulation can make absolute pollen counts uninterpretable. Therefore, corresponding dating of the sediment is desirable.

Once the pollen data have been obtained they have to be interpreted in terms of the vegetation they represent. There are many assumptions and errors at this stage. The main approach to limiting the errors here is to reconstruct the plant communities from fossil pollen assemblages using modern pollen spectra. The modern pollen spectra are collected from vegetation of known composition and this then enables vegetation composition to be estimated from the fossil assemblages. However, there are still two limitations. Firstly, the composition of vegetation is always changing and many modern vegetation communities did not exist in the past. Similarly many past vegetation communities do not have modern analogues. Secondly, differential preservation can make comparison between modern and fossil spectra difficult. One way round this is to concentrate on the changes in distribution of individual species (Huntley & Birks, 1983; Birks, 1989; Huntley *et al.*, 1989). In theory changes in the distribution of individual species can be used to infer previous climatic regimes. In practice, however, the background data on species autecology and pollen production often do not exist. For example, interpretation of the early Holocene *Juniperus* peak is limited by information on the autecology of *Juniperus* in addition to questions on the reliability of radiocarbon dating (Tipping, 1987). Species-environment relationships for predicting the distribution of key species under future climate scenarios are usually extrapolated from regression models which themselves make numerous assumptions.

With so many sources of error and underlying assumptions it is surprising that palynology is so widely practised. This must be put into context by looking at other available methods. Opportunities for using other methods such as macrofossils and dendrochronology are usually much more restricted geographically than those involving pollen. This is a result of the more ubiquitous nature of pollen and the wide distribution of preservation reservoirs. However, palynologists must strive to reduce or quantify as many of the errors and assumptions involved in the palynological process as possible. One of the most common ways of reducing errors in science is the use of replication. While replication at the regional level is common in palynology, even to the point were there is a redundancy in information (Walker, 1990), replication at the site level is

consistently lacking even though studies exist which have stressed the necessity of such replication because of variability in pollen deposition (Edwards, 1983; Whittington *et al.*, 1991). Despite recent advances in geochemical analysis and dating which are now commonly applied to support palynological studies, palynology cannot reach its full potential, nor answer the demanding questions of modellers, unless it is placed on a more rigorous scientific basis. To an extent some of the assumptions arising from the lack of replication can be overcome through techniques of bootstrapping and jack-knifing. These advances allow hypotheses to be generated from null models on the basis of pollen data, but cannot be used to refute null hypotheses which is the cornerstone of the scientific method. Alternatively, null models can be generated which produce testable hypotheses. This approach provides "strong inference" as opposed to the weak inferences normally associated with interperation of single cores (Hairston, 1989). As mentioned in the introduction, palynology is used throughout this thesis as a tool to answer questions on the dynamics of the treeline in relation to the environment and not simply to describe pollen cores. A detailed approach using replication on the small spatial scale of an individual woodland is the most appropriate approach for an ecological question of this nature.

While the use of pollen analysis to investigate climate-vegetation relations has become firmly established (Moore *et al.*, 1991) the role of other palynomorphs has not developed so rapidly. Rhizopods are testate amoebae (testaceans or thecamoebae) which are in the Subclass Testacealobosia within the Superclass Rhizopoda (Warner, 1988). Many species of rhizopod have tests that are well preserved in both peat and lake sediments (Tolonen, 1986) and display many distinct taxonomic features (Warner, 1988). Testae are composed of either organic material secreted by the amoebae or of preformed siliceous or calcareous plates. Some have exteriorous material such as mineral grains, fungal hyphea or diatom frustules (Sleigh, 1983). Tests of rhizopods from Creag Fhiaclach were very well preserved though definitive identification proved difficult in the absence of a reference collection. Keys from Corbet (1973) and Cash *et al.* (1905-1921), in conjunction with scanning electron micrographs from Ogden & Hedley (1980), were used in an attempt at identification. Originally the rhizopods were distinguished on the basis of their morphology. Four morphs were identified from Creag Fhiaclach and are described in Appendix II.

3.3 Pollen preparation

There is tremendous flexibility in the pollen preparation process, reflecting the highly variable nature of the matrices containing pollen. In addition to the many procedures outlined in introductory texts (Moore *et al.*, 1991; Faegri *et al.* 1989) pollen analysts frequently modify standard routines in order to get clearer preparations for counting. The procedures used in the preparation of samples for pollen analysis from Creag Fhiaclach were comparatively simple as the deposit consisted mainly of highly humified peat. The major problem in the preparation was the disaggregation of this tightly packed and highly humified matrix. Laboratory procedures were tested on two extra cores and are outlined below.

3.3.1 Laboratory method

Approximately 0.2 g of the air dried peat matrix was weighed into a Teflon-coated polypropylene test tube. Weight was used in preference to volume because obtaining accurate volume measurements for some sections of the core was impossible, for example, the unconsolidated litter layers and those peat layers which were high in granite crystals tended to crumble. To enable accurate sectioning of the litter layers it was necessary to freeze the cores and sample the litter layers while frozen. One cm^3 of standard pecan spore suspension was added to samples subjected to pollen analysis at this point. The only exception to this was the initial set of 24 modern pollen samples. This volume of the pecan spike was sufficient to give an approximate 1:2 marker to pollen ratio. The peat samples and spike were suspended in 10 cm^3 of cold 10 % KOH using a 'Whirlie' mixer for 10 s and left to stand overnight. The following morning the suspension was again 'Whirlie' mixed for 10 s. Pollen was separated from the remainder of the peat matrix by filtering. The KOH-peat suspension was passed through a 170 μm steel wire sieve, washed thoroughly by centrifugation and resuspended in distilled water. This process was repeated at least three times. Pollen was isolated from the supernatant by centrifugation at 4,000 rpm in a solid-head centrifuge. This was slightly faster then the 3,500 rpm recommended in Moore *et al.* (1991), but the pellet disintergrated less often at the slightly higher speed. The final centrifugation in water was at 5,000 rpm as the pellet often disintergrated at this stage. The duration of centrifugation varied according to the nature of the supernatant, i.e., KOH 10 mins, H_2O 15 mins and 20 mins for glacial acetic acid. Periodically the supernatant was checked to ensure that it contained no palynomorphs.

As the peat matrix was rich in organic colloids acetolysis was necessary. The procedure for the acetolysis is outlined in Appendix III. The unstained acetolysed pellet was then mounted in glycerol jelly. While mounting in silicone oil has the advantage of being able to turn the grains to aid identification, glycerol jelly, being solid, makes grains more easily relocated. In addition glycerol jelly is a much faster technique. The Ericoids were easier to distinguish when unstained and the pecan spike was obvious. Pollen were counted using a Medilux-12 microscope at × 600 magnification. Critical determinations were made using a Leitz Ortholux microscope at × 1000 magnification with oil immersion.

To reduce bias caused by experimental error, all samples from at least three cores were processed at once. Initially blind counts were used. However, this proved impracticable as occassionally additional slides had to be made and it was then necessary to know what the sample was. Subsequently more than one core was counted at a time and individual samples were placed in a random order before counting commenced.

3.3.2 Pollen identification

The principal key used in identification was that in Moore *et al.* (1991). Identification of palynomorphs was taken down to the level of species where this was possible. Reference was made to the pollen collection of the University of Edinburgh, and also to the pollen collection in the Palaeoecology Centre at Queens University Belfast to assist in distinction of the Ericoids. The identification of rhizopod taxa was difficult and is discussed in Appendix III.

3.4 Data reduction

One of the biggest problems in the interpretation of ecological data sets is to distinguish the noise component. This is especially true of pollen data. The origin of noise in ecological data can be multifarious and includes structures in the data at scales below that of immediate interest (Gauch, 1982). The object of data reduction is to elucidate data structures selectively and reduce noise to a minor component. Most of the information contained in ecological data can be described in a space of low dimensions (Goodall, 1954). Multivariate analysis is used to derive the dimensions likely to be of value in interpreting the data.

Multivariate analyses are geometric models where samples are points in multidimensional space. Axes (Principal Components) are fitted through the points, usually on the basis of orthogonal least squares. The first axis is the line of best fit through the points, and the second axis is the line of best fit through the residuals which is therefore at right angles to the first axis. The abundance of individual taxa are used to calculate the distance along the axes. Distances between samples are then Euclidean distances, as calculated by Pythagoras' theorem. A more complicated model can be applied by the use of standardisation and transformation. The eigenvalue is a measure of the amount of variance explained by the axis to which it relates. The first axis, having the best fit to the data, captures the most variation, the second axis the second most and so on. Correspondingly, the eigenvalues for each axis reduce sequentially. There can be as many axes in the data as there are species. The number of axes worthy of consideration depends on the magnitude of the eigenvalues and the nature of the data.

Ordination techniques are based on either linear or unimodal response models. Deciding which is appropriate can be done on the basis of the length of the first ordination axis. If the turnover in the first axis is less than two standard deviations the response curves can be considered approximately monotonic and linear methods of principal components analysis (PCA) and redundancy analysis (RDA) are appropriate. For gradients with more than two standard deviations of turnover unimodal-based methods should be utilised (Jongman *et al.*, 1987). Length of gradients as standard deviations are only routinely given in Detrended Correspondance Analysis (DCA). DCA was executed using the computer program CANOCO (ter Braak, 1987-1992). Pollen data were log-transformed (log (x+1)), otherwise default values were used. The pollen data covered a short gradient of 1.7 standard deviations of turnover.

Principal components analysis (PCA) and redundancy analysis (RDA) were applied to the pollen data from Creag Fhiaclach to determine the key trends in the data. PCA is an indirect gradient technique were the axes are assumed to represent latent environmental variables. As such PCA will find a gradient in the data even if there are no underlying environmental gradients. This possibility is reduced by canonical ordination techniques such as RDA. In RDA the axes are constrained to given environmental gradients by multiple regression. The first axis is the best fitting environmental variable or

combinations of environmental variables. This is the one which gives the smallest total residual sum of squares and the maximum regression sum of squares. Fitted values of the regression become the new site scores for the next iterative cycle. An excellent discussion of ordination and constrained ordination techniques is given in Jongman *et al.* (1987). However, RDA has all the basic assumptions of regression analysis. Variances of residuals are assumed to be constant and the species response model is assumed to be linear. To an extent these assumptions can be met by the log-transformation of the data and product variables can be used to improve on the linear model. PCA and RDA were executed using CANOCO version 3.0 (ter Braak, 1987-1992). The cores which were taken for pollen analysis were sampled in a grid design as described in Chapter 4. This imposes a geometric constraint on the data. To account for this, attributes such as altitude, replicate number and depth were entered as nominal environmental variables. Environmental variables are automatically standardised when read into CANOCO. Analyses were executed on the log transformed percentage data using the covariance matrix which was double centred by selecting the appropriate options in CANOCO. Pollen percentage data are commonly analysed using the covariance matrix (Bennett *et al.*, 1992).

3.4.1 Monte Carlo permutation tests

Often standard statistical tests cannot be applied to a given data set because one or more of the underlying assumptions cannot be ensured. Randomisation tests avoid the constraints of assumptions based on statistical distribution by generating empirical distributions from multiple resampling routines (Manly, 1992). The Monte Carlo permutation routine in CANOCO calculates the significance of the eigenvalue of the first axis or of the entire test. The test is based on a statistical comparison of the observed data with a set of random environment - species data generated from the original data set. This randomised data set is then ordinated in accordance with the observed data. Ordination of newly randomised data is repeated a large number of times, though 99 is the default value. The Monte Carlo significance factor is calculated simply by:

$$\frac{\text{no of simulated eigenvalues greater than or equal to the eigenvalue on the first axis or trace} + 1}{\text{number of requested permutations} + 1}$$

If the eigenvalue for the actual data set is in the top 5 % of the randomised data the result is significant at the 0.05 % level. An F ratio, without regard to covariables, is then calculated according to,

$$F = (sfce/q)/(rss/(n-p-1))$$

where sfce is the sum of first constrained eigenvalue; rss is the residual sum of squares; q is the number of environmental variables; n the number of samples; and p the number of covariables. The degrees of freedom are q for the numerator and (n-p-1) for the denominator.

3.5 Discriminant function analysis

Discriminant function analysis was used as a more objective method of classifying the fossil pollen spectra at Creag Fhiaclach into forest and heath assemblages than simple pollen quotients. Discriminant analysis finds the linear combination of taxa which produces the maximum difference between two formerly defined groups (Davis, 1986). Groups are separated so as to maximise the regression sum-of-squares and minimise the residual sum-of-squares (Jongman *et al.*, 1987). Distances between the means of groups are Mahalanobis distances (D^2). This is a Eucledian distance which takes account of the variance about the mean. As such it can be statistically tested using Hotelling's T^2 test or transformed to an F test. The discriminant function can then be used to allocate new samples to the *a priori* classification.

As with any process based on multiple regression, there can be as many linear additions to the discriminant function as there are variables. Stepwise discriminant analysis was used to extract the variables of use in distinguishing surface samples from Creag Fhiaclach. The selection of variables which contribute significantly to the function was decided on the basis of Wilks' Lambda U-statistic. The resultant function was then applied to classify the fossil spectra. Pollen data were arcsine transformed before analysis. Stepwise discriminant analysis was executed using routine 7M from the BMDP library of statistical programs (Dixon, 1985).

4

Calibration of recent pollen spectra and the treeline

4.1 Introduction

Interpretation and determination of pollen source areas are the most important aspects of modern pollen-rain investigations at high altitudes. Interpretation of sub-fossil pollen assemblages by reference to modern pollen assemblages has the basic assumption that modern vegetation types can be distinguished from their pollen spectra (Chapter 1). In the past this has been attempted on the basis of AP/NAP ratios. In the absence of an altitudinal gradient, AP/NAP ratios can be sensitive to vegetation structure on very small spatial scales (Sugita, 1994; Calcote, 1995). Turner (1964) hypothesised that the distance-decay relationship in *Pinus sylvestris* pollen representation from an isolated *Pinus sylvestris* stand at Cameron's Moss, Ayrshire was sufficiently sensitive to allow detection of small scale forest clearances. Similarly, the relative values of surface arboreal pollen were shown to be low in an area of *Calluna vulgaris* dominated heathland immediately juxtaposing a *Pinus sylvestris* stand in the Forest of Abernethy, Scotland by O'Sullivan (1973a). However, this approach becomes limited across altitudinal gradients as the arboreal pollen component can increase at high altitudes (Turner, 1964; Solomon & Silkworth, 1986; Fall, 1994).

A more quantitative approach developed by Maher (1963) is dependant on a linear regression model to calibrate treeline elevation from selected pollen taxa. However, the assumption of a linear relationship between the ratios observed and the distance from the treeline is dependant on the physiognomy of the vegetation. Where the physiognomy produces a relatively flat surface this assumption is probably met as only the relative densities of the selected pollen taxa will have an influence on the resolution of Suttons's equation as all other terms in the equation are constant. Therefore, differential distribution will be on the basis of density alone and this will give an exponential distance-decay function which when log-transformed produces a linear relationship. Where the

selected pollen taxa are from vegetation of differing aerodynamic surfaces this fundamental assumption may not be valid.

The *Pinus* treeline at Creag Fhiaclach is an abrupt boundary between forest and heath (see Section 2.6) and the relationship between the modern pollen-rain and the vegetation in relation to distance above and below the treeline is described here. The objective of this chapter is to calibrate the relationship between vegetation types and their associated pollen assemblages against altitude in a manner that will aid the interpretation of the sub-fossil pollen assemblages in a palynological study. The altitudinal distribution of *Calluna* flower density is also estimated.

4.2 Procedures

4.2.1 Modern pollen-rain

The relationship between the modern pollen-rain and position of the current treeline at Creag Fhiaclach was examined by extracting pollen from moss polsters. Carroll (1943) first extracted pollen from moss polsters to determine modern pollen deposition. The preservation state of pollen in moss polsters tends to be good because of the high humidity. Polsters are also free of problems associated with annual fluctuations in pollen production as they contain pollen from several years (Bradshaw, 1981). However, the modern pollen samples were collected in early spring before *Pinus* flowered to avoid the possibility of seasonal fluctuations Cundill (1985). Problems of redistribution should also be minimal. Pollen spectra from moss polsters should therefore, give an accurate measure of pollen deposition averaged over several years. The quantities of pollen produced and the spatial relationship between the polster location and distance from source should be the only major variables affecting the pollen spectrum.

Two points need to be considered in the experimental design of pollen-rain studies: the effective pollen source areas and spatial scales relevant to the changes that one is trying to detect (Gaudreau *et al.*, 1989). Lakes have too large a pollen source area to be of real use in detecting fine scale changes in treelines, especially in the Scottish Mountains were vegetation belts are much more compressed than in north America or continental Europe. Replication in space aids vegetation reconstruction from palynological data (Prentice, 1988).

In this study, four moss polsters, 30 m apart along the contour, were taken from each of nine altitudes to estimate spatial variation in pollen deposition (see Figure 2.3). Polsters were collected from the lowest six altitudes in February 1992 and from the next three altitudes in April 1994. In addition to the moss polster samples a litre of snow was collected from the Ciste Mhearad (Grid Ref: NJ 012 045, see Figure 4.1) snow bed in August 1993. The nature of the vegetation at each altitude sampled is shown in Table 4.1. All moss polsters were 5 cm x 5 cm and were composed mostly of *Hylocomium splendens*. Only green parts of the moss polsters were used for extracting pollen. These contain pollen from several years, reducing annual fluctuations in the pollen influx, whereas, use of the entire depth of the polster introduces the problems associated with differential preservation (Bradshaw, 1981). The mean oven dry weight (± SE) of polsters was 2.7 g ± 0.4 g. The moss polsters were shaken in 100 cm^3 of 10% KOH, boiled for 20 minutes and washed through a 170 μm sieve. After extraction, pollen was prepared for counting using standard techniques as described in Chapter 3.

Table 4.1: Summary of altitudes sampled and associated vegetation/substrate. Altitudes for the lowest six sites are means of seven measurements from an aneroid barometer. The highest altitude was estimated from an ordnance survey map. The height at 840 m was level to an ordnance survey spot height at the Argyll Stone (NH 905041). The two sites immediately below the highest were evenly spaced between the Argyll Stone and the previously recorded highest site and their altitudes were estimated accordingly.

Altitude	SE (n = 7)	Vegetation	Date collected
1100 m	-	Late lying snow bed	3-8-93
840 m	-	Montane *Calluna* heath	14-4-94
812 m	-	" " "	14-4-94
785 m	-	" " "	14-4-94
758m	13	Upland *Calluna* heath	5-2-92
717m	8	" " "	5-2-92
707m	11	" " "	5-2-92
648m	14	Treeline - small scale mosaic	5-2-92
624m	11	*Pinus* forest	5-2-92
606m	14	" "	5-2-92

Five slides were initially made from one polster at each of the six lowest altitudes. As pollen from individual taxa tend to distribute at different rates across the slide during mounting (Brookes & Thomas, 1967) three traverses were made across each of these slides. A nested analysis of variance (Table 4.2) showed that the between-polster

variation in percentages of *Pinus* pollen was much greater than variation between slides for the same polster. Subsequently, only one slide and three traverses were made from each of the remaining polsters. All traverses were made blind.

Table 4.2: Variance estimates in pollen quotients from moss polsters.

Source of variation	d.f.	SS	MS
Between polsters	5	842.9	168.6
Between slides	24	82.6	3.4
Between traverses	60	1105.2	18.4
Total d.f.	89		

4.2.2 Estimates of *Calluna* flowering density

Calluna flowers were counted annually in the first week of September from up to eight altitudinal contours for three years. In the first year, 1992, only six altitudes were sampled. These were the altitudes from which moss polsters had been collected to calibrate the modern pollen-rain. In the subsequent years two additional altitudes were sampled to give a greater resolution around the treeline.

As *Calluna* flowering can be extremely patchy numbers of flowers were averaged from five 10 cm x 10 cm sub-samples chosen randomly from one 1 m x 1 m quadrat. In total, flowers were counted from 15 1 m x 1 m quadrats in 1992 at 10 m intervals along the contours. In 1993 and 1994 the number of quadrats was reduced to 5 at 30 m intervals to match the sampling design in the modern pollen-rain study.

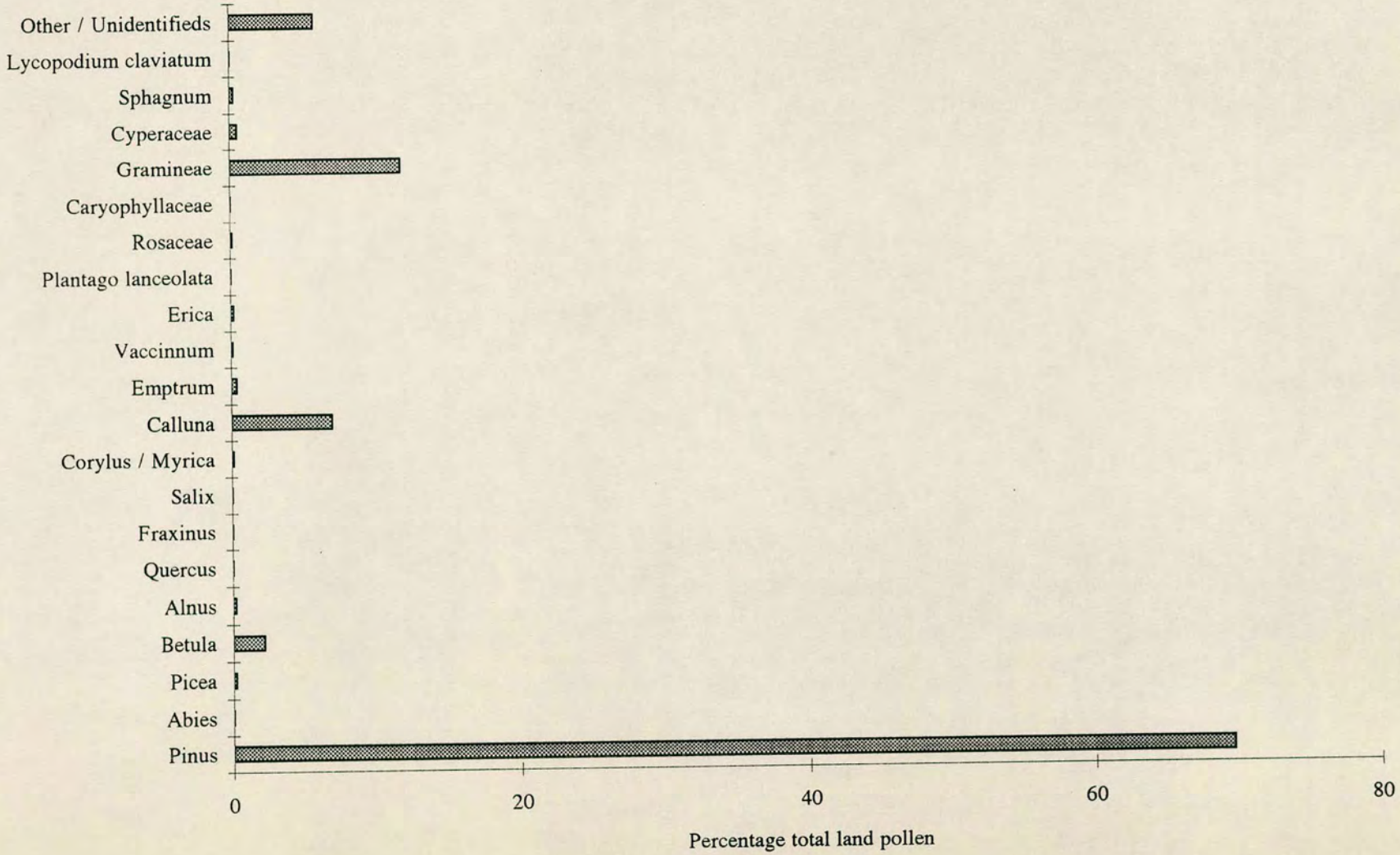
4.3 Results

4.3.1 Modern pollen-rain

Pinus and *Calluna* comprised 96% of the palynomorphs recorded. The remaining taxa were mainly *Betula*, Gramineae and Cyperaceae. The minor taxa together comprised less than five per cent of the total pollen. *Pinus* pollen was expressed as a percentage of the *Pinus* + *Calluna* total (P*100/(P+C)) to give quotients. Mean pollen sums ($\pm$ SE) were 2330 $\pm$ 320 for the polsters that had five slides prepared and 350 $\pm$ 25 for the remainder.

Below the treeline the representation of *Pinus* pollen in the forest was high. The P*100/(P+C) quotient declined abruptly at the treeline, but above the treeline it increased

Figure 4.1: Full pollen spectrum for the Ciste Mhearad snow bed at 1100 m a.s.l in the Cairngorms, expressed as total land pollen. The sample was collected on 3 August 1993. *Pinus* was by far the most abundant pollen type, with *Calluna* and Gramineae being the next most common types. There were a large number of pollen grains which were mechanically damaged and difficult to identify.



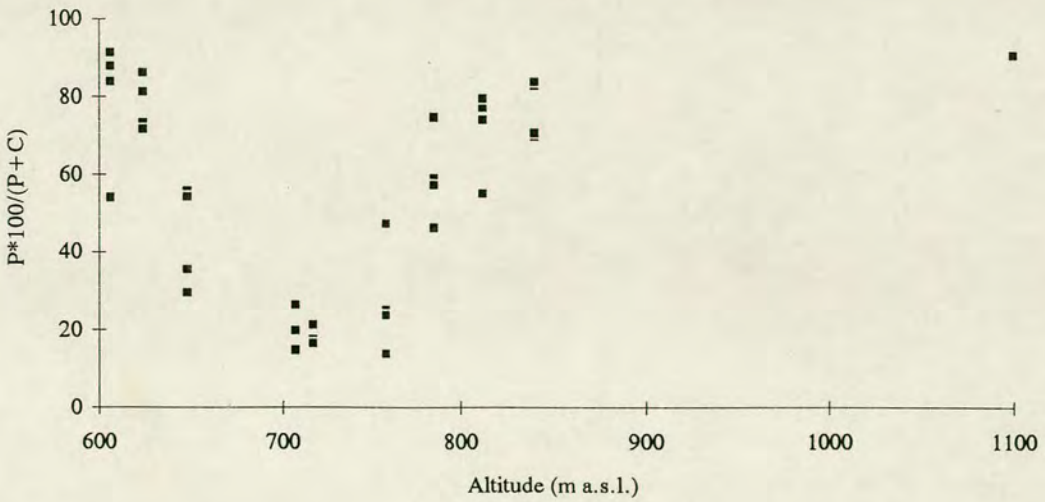
with altitude. This quotient reached 90% at 1100 m as was determined from the snow bed sample. The full spectrum from Ciste Mhearad is shown in Figure 4.1. The large number of unidentified grains was a result of mechanical damage. The P*100/(P+C) pollen quotient differed significantly with altitude ($p < 0.0001$, ANOVA, angular transformation, Table 4.3).

Table 4.3: Analysis of variance of *Pinus* pollen in moss polsters expressed as the angular transformation of P*100/(P+C). Comparison of means of four replicates at each of nine altitudes.

Source of variation	SS	df	MS	F	P-value
Between altitudes	7906.6	8	988.3	20.8	<0.0001
Within altitudes	1284.9	27	47.6		
Total	9191.4	35			

The P*100/(P+C) pollen quotient can be seen from the modern pollen-rain to rise with distance above the treeline, but below the treeline the representation of *Pinus* pollen in the forest was high (Figure 4.2). This quotient reaches very high values at 1100 m as was determined from the snow bed sample above.

Figure 4.2: Change in representation of *Pinus* in the pollen spectrum with altitude at Creag Fhiaclach. The treeline is at 648 m. Quotients from the lowest nine altitudes were derived from moss polsters. The quotient at 1100 m was derived from snow in the Ciste Mhearad snow bed.



4.3.2 Distribution of *Calluna* flower density

The distribution of *Calluna* flowering was very similar in all three years. Within the forest numbers of flowers did not exceed 10,000 m^{-2} during the three years (Figure 4.3). Flowering peaked significantly at the treeline (648 m) in all years. At higher altitudes flowering density gradually decreased. An analysis of variance on the density of flowers showed highly significant differences between altitudes in all three years (Table 4.4).

Figure 4.3: Variation in *Calluna* flowering with altitude. In 1992, flowers were counted from the six lowest altitudes spanning the treeline. In both 1993 and 1994, two extra altitudes were sampled to give greater resolution around the treeline. Comparison of 15 means in 1992 and 5 means in 1993 and 1994, standard errors are shown as error bars. The value for 606 m in 1993 is so low (0.4 ± 0.4) that it is not shown in the figure.

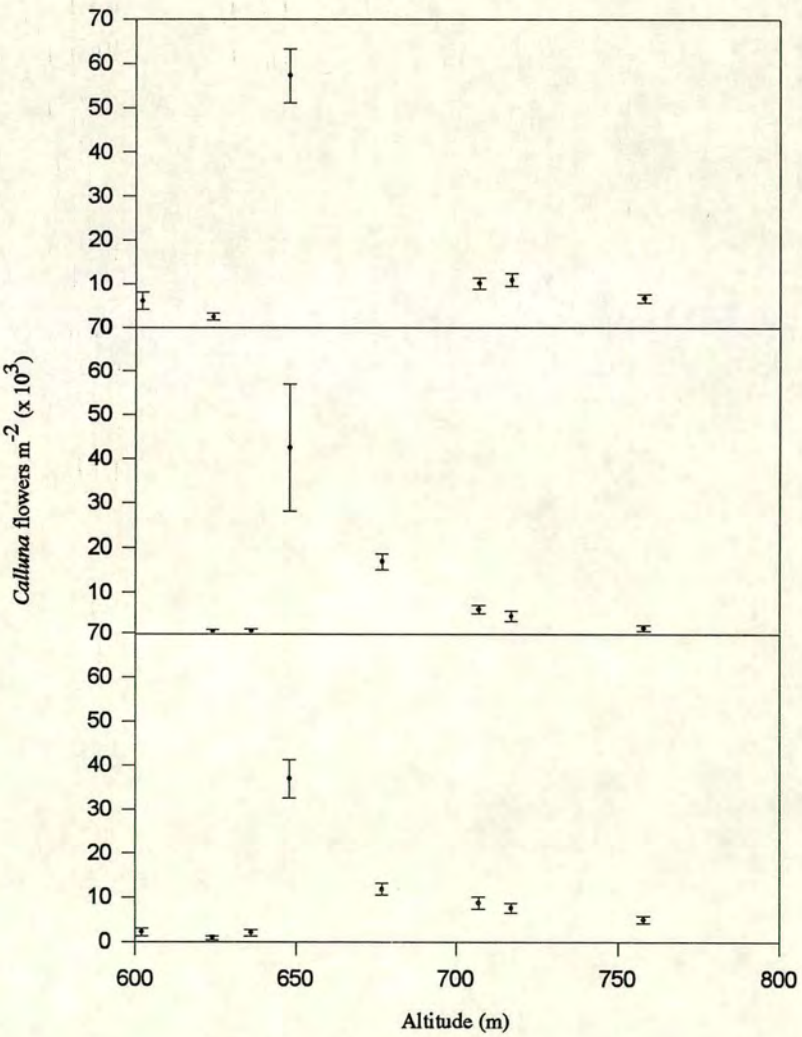


Table 4.4: Analysis of variance comparing mean *Calluna* flower density between altitudes in 1992, 1993 and 1994.

1992

Source of Variation	SS	df	MS	F	P-value
Between altitudes	7971708	5	15943422	55.09	< 0.0001
Within altitudes	24310689	84	289413		
Total	104027796	89			

1993

Source of Variation	SS	df	MS	F	P-value
Between altitudes	18245646	7	2606521	7.75	< 0.0001
Within altitudes	10763040	32	336345		
Total	29008686	39			

1994

Source of Variation	SS	df	MS	F	P-value
Between altitudes	12071919	7	1724560	41.84	< 0.0001
Within altitudes	1318821	32	41213		
Total	13390740	39			

4.4 Discussion

4.4.1 Modern pollen-rain deposition at the treeline

The significant relationship between the P*100/(P+C) pollen quotient and altitude reflects the transition from *Pinus* forest to *Calluna* heath. Both *Calluna* and *Pinus* are copious pollen producers. *Calluna* can produce 2,000 pollen grains per anther (Erdtman, 1969) with eight anthers per flower, while *Pinus* can produce 158,000 grains per flower (Pohl, 1937 in: Birks & Birks, 1980). *Pinus* pollen is released high into the air stream and tends to travel long distances. As the spatial scale of this study in relation to distance from the treeline is relatively small, it is unlikely that a change in the absolute density of *Pinus* pollen explains the sudden decrease in *Pinus* percentage at the treeline. When using relative pollen data the percentage for an individual taxon is dependent on the abundance of the other taxa. If the abundance of one taxon increases dramatically, the relative abundance of the other taxa must decrease because of the percentage constraint. The absolute abundances of the other taxa may not actually change. The only other species at

Creag Fhiaclach which could produce sufficient quantities of pollen to influence the pollen sum is *Calluna*.

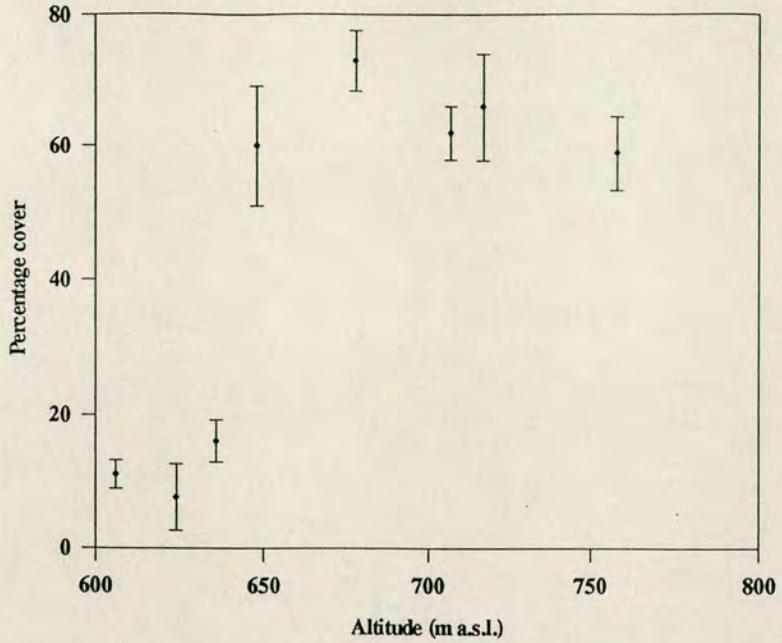
4.4.2. Variation in *Calluna* flowering with altitude

The modern pollen-rain study demonstrated a significant decrease in the representation of *Pinus* pollen at the forest-heath interface. The P*100/(P+C) quotient is obviously sensitive to the contribution of both *Pinus* and *Calluna* to the pollen spectrum. The decline in the quotient above the treeline can be a function of the reduction in *Pinus* pollen or an increase in *Calluna* pollen. Hence, the observed relationship between representation of *Pinus* pollen and altitude can, alternatively, be interpreted in terms of the distribution of *Calluna* pollen.

Reducing light to 12.25% of that in the open can significantly reduce flowering in *Calluna* ($p < 0.001$) within one growth season (Hester, 1987). Lignin production also declines significantly in shade ($p < 0.01$) over two growth seasons (Iason & Hester, 1993). Below the treeline at Creag Fhiaclach shade from the forest effects the abundance, vigour and flower production of *Calluna*. Low density of flower production is illustrated in Figure 4.3. During the vegetation survey of Creag Fhiaclach in September 1993 abundance of *Calluna* as percentage cover was measured. *Calluna* abundance was below 15% in the forest (Figure 4.4), rising to 60% at the treeline and maintaining an abundance of at least 60% to the highest altitude measured. *Calluna* growth form also differed from forest to heath. Plants in the forest were more lush, green and less woody, with a sprawling growth habit, whereas *Calluna* plants from the open heath were heavily lignified, erect plants with a dense canopy. Thus, reduced abundance and suppression of flowering in *Calluna* because of shade at the two lowest altitudes contributed to high P*100/(P+C) quotients.

In open heathlands flowering density of *Calluna* is negatively correlated with altitude (Miller & Watson, 1978). This reduction in flowering contributes to the gradual rise in percentage of the more uniformly distributed *Pinus* pollen with distance from the treeline.

Figure 4.4: Altitudinal variation in the abundance of *Calluna* at Creag Fhiaclach in September 1993. Values are means of 5, with standard errors shown as error bars.



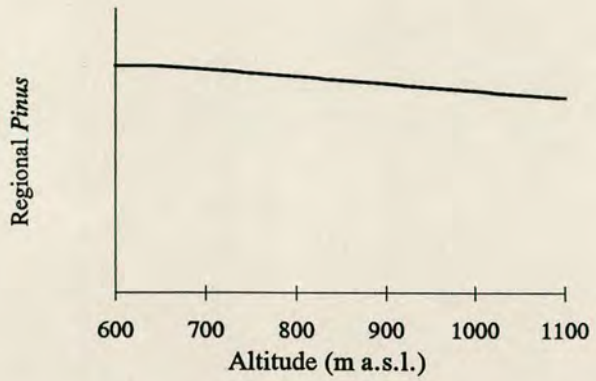
The very low P*100/(P+C) quotients at the treeline are probably derived through shelter from scattered *Pinus* and *Juniperus communis* close to the treeline resulting in a peak in *Calluna* flowering and pollen production. Shelter has been shown to increase flowering of *Calluna* significantly over a small spatial scale in the Cairngorms (Bayfield, 1984). Density of flowering around the treeline was highly variable. This was because the 'treeline' is not a straight line. Some quadrats from the treeline altitude will have been recorded from vegetation dominated by *Pinus* and some from shrub dominated vegetation. This explains the high variability in the P*100/(P+C) quotients from samples at the treeline (Figure 4.2).

4.5 Effective pollen source areas at the treeline

The modern pollen-rain at Creag Fhiaclach is the amalgamation of pollen from different sources, with different corresponding source areas being deposited through different processes. These will be examined individually below, with accompanying sketch diagrams.

1) Regional pollen, has a high *Pinus* component, which declines only slightly with incresing altitude (Figure 4.5). That the high *Pinus* representation at higher altitudes was

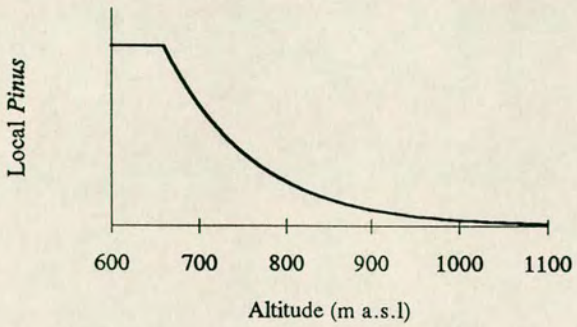
Figure 4.5: Schematic diagram indicating the hypothesised dominant influence of region al *Pinus* pollen in the pollen rain. The quantity of Pinus pollen is assumed to decline slightly with altitude.



caused by regional pollen rather than the stand at Creag Fhiaclach is supported by the pollen spectra from Ciste Mhearad where *Pinus* pollen at 70% of TLP predominates. Pollen from the snowbed site is 4 km from the nearest *Pinus* stands which are to the north at Glen More Forest. The nearest *Pinus* stand to the west of Ciste Mhearad is 7 km away on the Rothiemurchus Estate. The immediate vegetation is very sparse and dominated by low pollen producers. There is also a very high percentage of bare ground. This snow bed spectrum is the regional pollen signal. As the regional pollen signal has a very dominant *Pinus* component the contribution of the local *Pinus* stand to the modern pollen spectra at Creag Fhiaclach is likely to be small in comparison. The 90% regional *Pinus* pollen is comparable to the 80% AP found by Spear (1989) in the alpine zone of the White Mountains in north America.

2) Exponential decline of local *Pinus*. There will be some influence on the quotient from the adjacent *Pinus* stand corresponding to Turner's β component (Turner, 1964; Figure 4.6). Arboreal pollen has been assumed to decline exponentially with distance at forest ecotones in other studies (Table 1.1). At Creag Fhiaclach the distance between the treeline and the altitude sampled immediately above it (707 m) are within the distance over which a 50% decline in arboreal pollen has been detected elsewhere (Table 1.1). This can be seen in the pollen deposition at Creag Fhiaclach were there was an altitudinal discrepancy between the pattern of *Calluna* flower density and the P*100/(P+C) pollen quotients. *Calluna* flower density peaked exactly at the treeline (Figure 4.3) but the

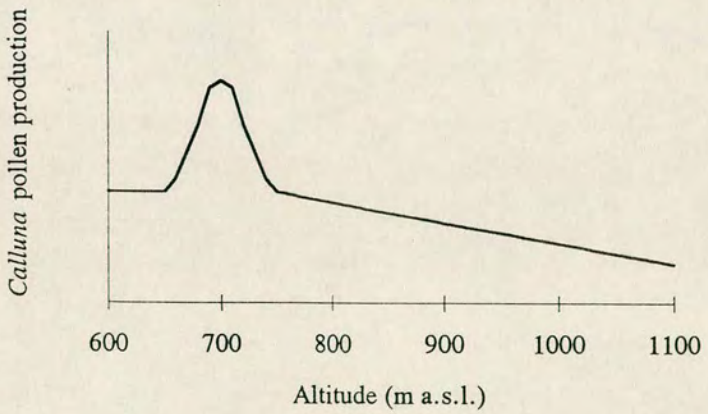
Figure 4.6: The expected exponential reduction with altitude in deposition of *Pinus* pollen orginating from the *Pinus* stand at Creag Fhiaclach.



lowest P*100/(P+C) pollen quotients were not detected until 707 m and stayed low until 758 m (Figure 4.2).

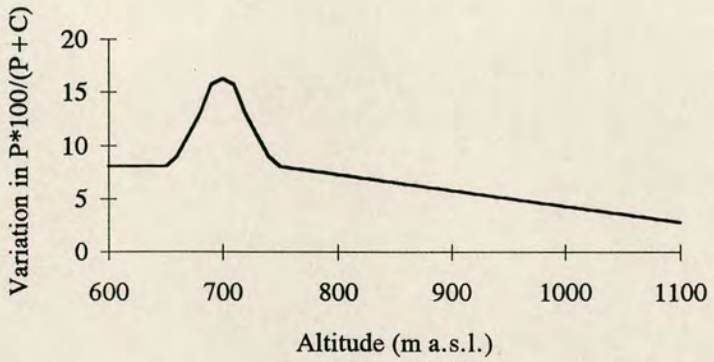
3) Variation in the production of *Calluna* flowers with altitude influences the quantity of *Calluna* pollen (Figure 4.7).

Figure 4.7: Assumed changes in absolute *Calluna* pollen deposition with altitude at Creag Fhiaclach. Pollen deposition is low within the forest, maxium in the shelter above the treeline and then declines with increasing altitude above the treeline.



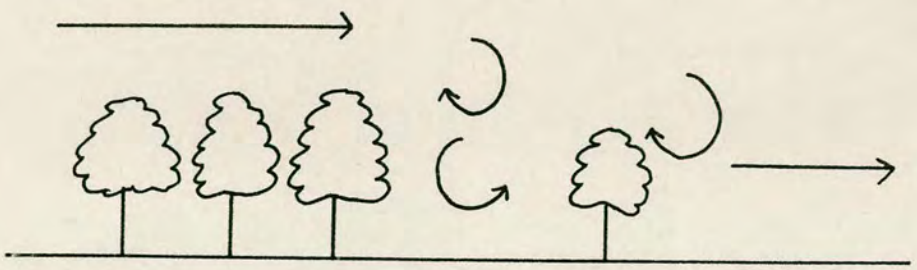
4) Increased heterogenity of vegetation at the treeline will result in coresponding variation in the P*100/(P+C) quotient. This idea is developed further in Chapter 6.

Figure 4.8: This graph depicts the changes in the P*100/(P+C) quotient with altitude. Within the forest the variation in the modern pollen rain will be constant throughout the forest, reflecting the uniformity of the habitat. At the treeline, the greater variation in the vegetation will result in more heterogeneity in pollen deposition. Above the treeline the variation in the pollen quoitents vegetation will reduce with altitude as the *Calluna* heath becomes more uniform in structure and composition.



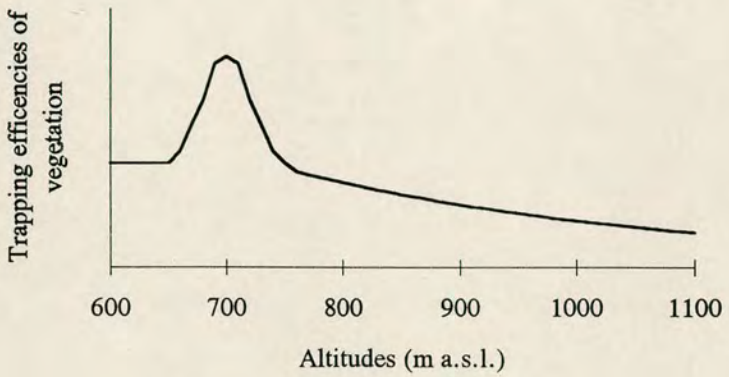
5) Turbulence effects increasing *Pinus* pollen deposition at an irregular forest edge (Figure 4.9). Impaction has been long recognised to influence deposition of particles suspended in air (Gregory, 1961). The high wind speeds and the irregular nature of the vegetation immediately at the treeline will influence the process of impaction.

Figure 4.9: The structure of the forest at the treeline creates conditions for eddy formation which will influence pollen deposition through impaction.



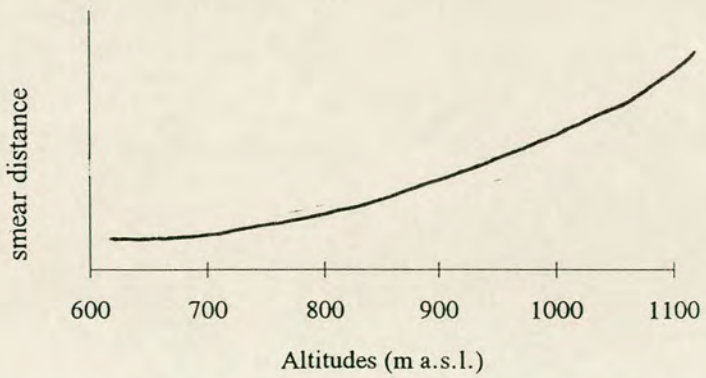
6) Similarly, taller dense *Calluna* and *Juniperus communis* trap *Pinus* pollen with greater efficency just above the treeline.

Figure 4.10: Efficiency of pollen trapping is a combination of impaction and re-deposition. Thus trapping efficiencies will be moderately good under the *Pinus* canopy as pollen once it has impacted will tend not to be re-deposited in the relatively non-turbulent environment. At the treeline efficiency of trapping will be high as impaction increases because of the structural changes in the vegetation (see Figure 4.9). With greater coupling between vegetation and wind above the treeline re-deposition will reduce trapping efficiencies.



7) Wind smearing of the locally produced *Calluna* pollen will occur at altitudes above the shelter at the treeline as the vegetation canopy becomes increasingly coupled to the atmosphere (Figure 4.11).

Figure 4.11: Schematic diagram showing how the distance over which the *Calluna* pollen signal can be smeared through re-deposition in an increasingly turbulent environment.



This will also contribute to the altitudinal discrepancy between the variation in *Calluna* flower density and the P*100/(P+C) pollen quotients as outlined in point two above.

Pinus pollen in this study, has two effective source areas. The constant regional source area which is in the order of kilometres (1 above) and a much smaller source area from the immediate stand at Creag Fhiaclach (2). The *Pinus* quotient is rapidly attenuated by the dense *Calluna* flowering in the sheltered environment at the treeline (3). The effective pollen source area for *Calluna* is very small at the treeline, of the order of one metre as will be shown later in Chapter 6, this concurs with the results of Evans & Moore (1985). The small source area of *Calluna* means the increased heterogenity of the vegetation at the treeline caused by the diffuse band of *Juniperus communis* (4) will influence the pollen quotients. The influences of the remaing factors influencing pollen deposition at the treeline (5-7) will be difficult to quantify.

Thus, the altitudinal variation in the P*100/(P+C) quotient at Creag Fhiaclach is not a simple function of the exponential decline in *Pinus* pollen with distance from the forest edge. The changes in the observed P*100/(P+C) quotient above the treeline were primarily caused by the variation in the local production of *Calluna* pollen. Inherent in this argument is the assumption that *Pinus* pollen forms a substantial background influx over the entire study area.

Records of long-distance transport and high background levels of *Pinus* pollen are notably common (Huntley & Birks, 1983; Bennett, 1984; MacDonald & Ritchie, 1986; Schwartz, 1989). The aptitude for long distance transport of *Pinus* pollen and the high altitude of the site contribute to the hypothesis that the *Pinus* pollen in all the polsters above the treeline is mostly regional as defined by Janssen (1966). This pronounced regional *Pinus* pollen signal has an approximately uniform distribution. In addition, the regional components of pollen spectra become more pronounced with altitude (Markgraf, 1980; Schwartz, 1989; Fall, 1992). Fall (1992) found this was particularly true for *Pinus* pollen.

Caseldine (1981) found local *Calluna* pollen production confounded the extra-local pollen signal in the treeless centre of Bankhead Moss, Scotland. Occasional large clumps of *Calluna* pollen were found in the pollen slides from Creag Fhiaclach, again indicating a local effective pollen source area. The effective source area of *Calluna* will increase with

distance above the treeline as the canopy boundary layer becomes more tightly coupled to the higher wind speeds (Wilson *et al.*, 1987).

Rapid attenuation of percentage arboreal pollen by locally deposited Ericaeous pollen taxa has been observed in other studies in Scotland. O'Sullivan (1973a) found representation of *Pinus* to be 75-85% in moss polsters from within pinewoods, dropping to 55-65% in small clearings, 30-40% in heath with scattered trees and 20-45% in open heath at Abernethy. These changes in the decline of *Pinus* with reduction of cover was associated with a corresponding increase in *Calluna* representation. *Juniperus communis* had very low representation in all samples with the highest value 6%. O'Sullivan interpreted the changes in *Pinus* representation as the assemblages within the forest canopy being mostly derived from locally deposited arboreal pollen similar to Creag Fhiaclach. Pollen assemblages in the clearings are described as being extra-local pollen (*sensu* Janssen, 1966), however in the absence of dimensions this is difficult to ascertain. In the scattered pine heath there is considerable variation in *Pinus* representation. O'Sullivan (1973a) states that AP rises where there are trees and decreases where there are none, but again no distances are given. O'Sullivan's lack of a detailed vegetation description makes it difficult to determine pollen source areas from his data, though the overall scale of the study area was small. *Betula* representation has also been shown to decline dramatically from 76-50 % within Craigellachie birch wood, Speyside to 35% in a small clearing (Goddard, 1970), though again dimensions were not given. On an altitudinal gradient at Rannoch Moor (Ward *et al.*, 1987) found that *Pinus* pollen frequencies dropped to as low as 1% within 100 m above the forest edge in *Calluna* - *Erica* dominated ground flora.

4.6 Implications for palynological study.

4.6.1 Use of pollen quotient to detect historic treelines

Fine spatial resolution sampling at Creag Fhiaclach was necessary to detect the changes in the pollen source areas over the very short vegetation gradients at the treeline. Change in the P*100/(P+C) quotient with altitude was not linear or exponential in contrast to the *Pinus*/*Picea* ratio of Maher (1963). Maher assumed that *Pinus* was regional and deposited at a constant rate and therefore, the more quickly deposited *Picea* pollen could indicate distance above the treeline. However, Maher's approach does not allow for the change in physiognomy at the Creag Fhiaclach treeline. The high background *Pinus* pollen at Creag

Fhiaclach also restricts the use of a simple regression model or the extended R-value model.

The modern pollen-rain demonstrates the potential of simple pollen quotients to detect historic treeline fluctuations. The forest samples have an overall mean (± SE) of 79% (± 4%, n=8) *Pinus* expressed as P*100/(P+C). This contrasts strongly with the pollen spectra from open heath at 707-758 m above the current treeline, where the mean was 23% (± 3%, n=12) *Pinus*. High altitude heath from above 780 m, however, also has a high P*100/(P+C) quotient of 50-80%. Consequently, any sub-fossil pollen spectrum from this site with a *Pinus* pollen percentage below 30% can be considered to represent a heath pollen assemblage typical of vegetation immediately above the treeline. Pollen spectra with *Pinus* pollen percentages above 30% can be derived from either forest or montane heath vegetation.

4.6.2 Optimal sampling and experimental design

Spatial variability in modern pollen-rain from terrestrial sites due to local depositional events can be considerable (Adam & Mehringer, 1975). Replication should be applied to reduce the standard error of the sample means as efficiently as possible. The most efficient level of replication is one that will minimise Type II errors by giving a test statistic that is just sufficently powerful to reject the null hypothesis if the working hypothesis is true (Underwood, 1990)

This study showed a difference in the P*100/(P+C) pollen quotients of forty-five per cent between forest and heath vegetation at 707-758 m. Hence the maximum permissible standard error in relative pollen counts to detect the treeline should be less than 45/t. The value of t depends on the number of degrees of freedom. In the modern pollen-rain study the total degrees of freedom are 23, being 6 - 1 for altitude and 6(4 - 1) for residuals. Table 4.5 shows the largest acceptable standard errors associated with the observed variance and these degrees of freedom. The target standard error in this case was put at the more conservative levels of 8% and 5% respectfully.

Table 4.5: Largest acceptable standard errors for distinguishing forest from heath using a one tailed t test based on the sampling design described in Section 4.2.1.

	df	t	S.E.
5% level	23	1.71	13
1% level	23	2.50	9

Pollen analysis is a very time consuming process. In palynological studies, sampling strategies which reduce the residual error with the minimum number of replicates should be sought. Each stage in the sampling procedure (taking cores, preparing slides, counting transects across slides) has an associated error and cost in processing time. At the primary level, the time spent collecting and pre-treating samples must be justified by reducing the standard error of the mean pollen percentage within each altitude. Similarly, at the secondary level time taken to prepare slides from each sample must be optimised in terms of variance. At the tertiary level the pay-off is between the number of transects across each slide and the variation between transects. The allocation of resources does have an optimal solution in terms of time or desired variance. This optimum is found by minimising the product of the following equation from Snedecor & Cochran (1967):

$$VC = \left(\frac{s_1^2}{n_1} + \frac{s_2^2}{n_1 n_2} + \frac{s_3^2}{n_1 n_2 n_3} \right) \cdot (c_1 n_1 + c_2 n_1 n_2 + c_3 n_1 n_2 n_3)$$

Where VC is the product of variance and cost; s_1^2 is the variance associated with sampling at the primary level, i.e., variance between cores; n_1 is the number of samples taken at the primary level and c_1 is the cost in time associated with each primary sample. Similarly for the secondary and tertiary levels.

Using the variance estimates from the modern pollen-rain data, the optimum number of replicate cores to be taken at each altitude for a palynological study can be calculated. Table 4.6 shows optimal solutions at the 5% and 1% significance levels.

A target SE to permit rejection of the null hypothesis at 5% significance gave an optimal solution of 8 cores at each altitude, with one slide from each pollen sample and two counts across each slide. The total cost was 1120 minutes per altitude. Increasing the acceptable

level of significance to 6% saved 280 minutes per altitude, reducing the number of samples to 5 while still requiring one slide from each polster and three counts across each slide. As a significance level of 6 % is still well within the limit of 8%, the number of replicate cores to be collected within each altitude for the palynological study was set at five.

Table 4.6: Optimal sampling solutions for a palynological study at Creag Fhiaclach. The variance estimates for each level in the sampling design and the associated costs are given in columns 2 and 3. The optimal number of samples to reach given maximum standard errors are in the final three columns along with actual variances, standard errors and total costs. Number of samples are rounded up to the largest whole sample.

			8% level	6% level	5% level
	Variance	Costs (min)	Samples	Samples	Samples
Replicates	168.6	70	3	5	8
Slides	3.4	10	1	1	1
Transects	18.4	30	2	2	2
		Total variance	60.4	30.2	22.7
		Total cost	420.0	840.0	1120.0
		SE	7.8	5.5	4.8

4.6.3 Implications for pollen sum

Pollen counts in the literature for the British Isles usually range between 500-1000 TLP. In this instance a smaller pollen count was adequate. These upland pollen spectra were species depauperate with a total of 26 taxa being encountered. The size of the pollen sum was also decided by the modern pollen-rain study. The primary aim of the palynological study (Chapter 5) was to obtain *Pinus* pollen quotients and the qualitative aspects of the data set were deemed less important. The *Pinus* quotients from polsters where a count of 1500 was made did not differ significantly from the remaining three polsters in any altitude where the pollen count was 300. However qualitative differences in the pollen diagrams may arise. Faegri & Iverson (1975) illustrated the effect of a small pollen sum on pollen diagrams. Subsequently, minimum pollen sums were either:

- 300 total pollen if *Pinus* composed less than 50% TLP,
- 300 *Pinus* if *Pinus* was more than 50% TLP,
- a minimum of two transects across each slide.

5

Palynological Study

5.1 Introduction

Positions of treelines in the Cairngorms throughout the current post-glacial have been broadly correlated with climatic maxima and minima. However, most of the evidence for previous treeline positions is strongly based on the evidence obtained from *Pinus* stumps. As the spatial and temporal distribution of stumps indicates only the preservation record, much detail on the history of treelines in the region is still required. The highest and most intact treeline left in the Cairngorms is at Creag Fhiaclach. The modern pollen-rain study (Chapter 4) demonstrated that the current treeline at Creag Fhiaclach can be identified from a significant change in the P*100/(P+C) pollen quotient. P*100/(P+C) pollen quotients are used here to investigate previous treeline fluctuations at Creag Fhiaclach. As the modern pollen-rain study also demonstrated the variability of P*100/(P+C) pollen quotients in the heterogeneous depositional environment at the treeline is such that replicate cores were necessary in this study. This Chapter describes the pollen profiles from Creag Fhiaclach and the variation in the P*100/(P+C) pollen quotient with both depth and altitude and also identifies the major trends in the palynological data using multivariate techniques. The discussion concerns the variation and interpretation of the data. Interpretation in terms of treeline dynamics is discussed in Chapter 8.

The hypothesis tested is that there has been no change in treeline elevation with time. The null hypotheses tested were defined on the basis of modern pollen quotients:

H_{o1}: Modern pollen distribution is representative of the altitudinal distribution at all depths down the cores.

H_{o2} : Change in position of the transition between forest and heath-type pollen spectra occurs at the same altitude at all depths.

To refute H_{o2} it is necessary to demonstrate that at particular ages the point of transition in the pollen quotients was at different altitudes at different times. If H_{o2} is false then H_{o1} must also be false.

5.2. Field Methods

On 16 May 1992, five replicate peat cores were taken from the six lowest altitudes, previously sampled for moss polsters (see Figure 2.3). Replicates were 30 m apart along the contour. Peat cores were taken using 4 cm x 4 cm electrical trunking cut to 50 cm lengths, which were supported by a metal brace. This trunking has an advantage over drain piping in that one side is detachable. Only the three sided section was used when the trunking was pushed into the peat, leaving the peat core attached to the main body of peat. A very sharp knife was then used to sever the peat core. The detached side of the trunking was replaced *in situ* before the isolated core was extracted from the peat body. This procedure reduces compression of the peat during sampling. Once extracted the cores were sealed with masking tape. On the following day they were also wrapped in cellulose film and put into cold storage at 4 °C.

5.2.1 Sub-sampling for pollen preparation

The 4 cm x 4 cm cores were frozen overnight before being removed from the electrical trunking. To reduce vertical smear effects, which may have occurred when the trunking was pushed into the peat, clean sections of peat were prepared. This was done by cutting across the peat faces horizontally with a sharp scalpel. The scalpel was thoroughly cleaned between each cut. Cores were sub-sampled at 5 mm intervals. Sampling interval was to be chosen on the basis of tephra distribution at the site but insufficient tephra was found to proceed with this principle (Chapter 7). The sampling interval was therefore chosen on the basis of reported tephra distribution in lowland peats, where tephra bleeding is limited to 3 mm (Valerie Hall, pers.com.). The litter layers were sub-sampled while the cores were still frozen. Expansion of the core on freezing was negligible and therefore unlikely to be a source of error. Alternate samples were used for pollen preparation as described in Chapter 3. In all 482 pollen counts were made.

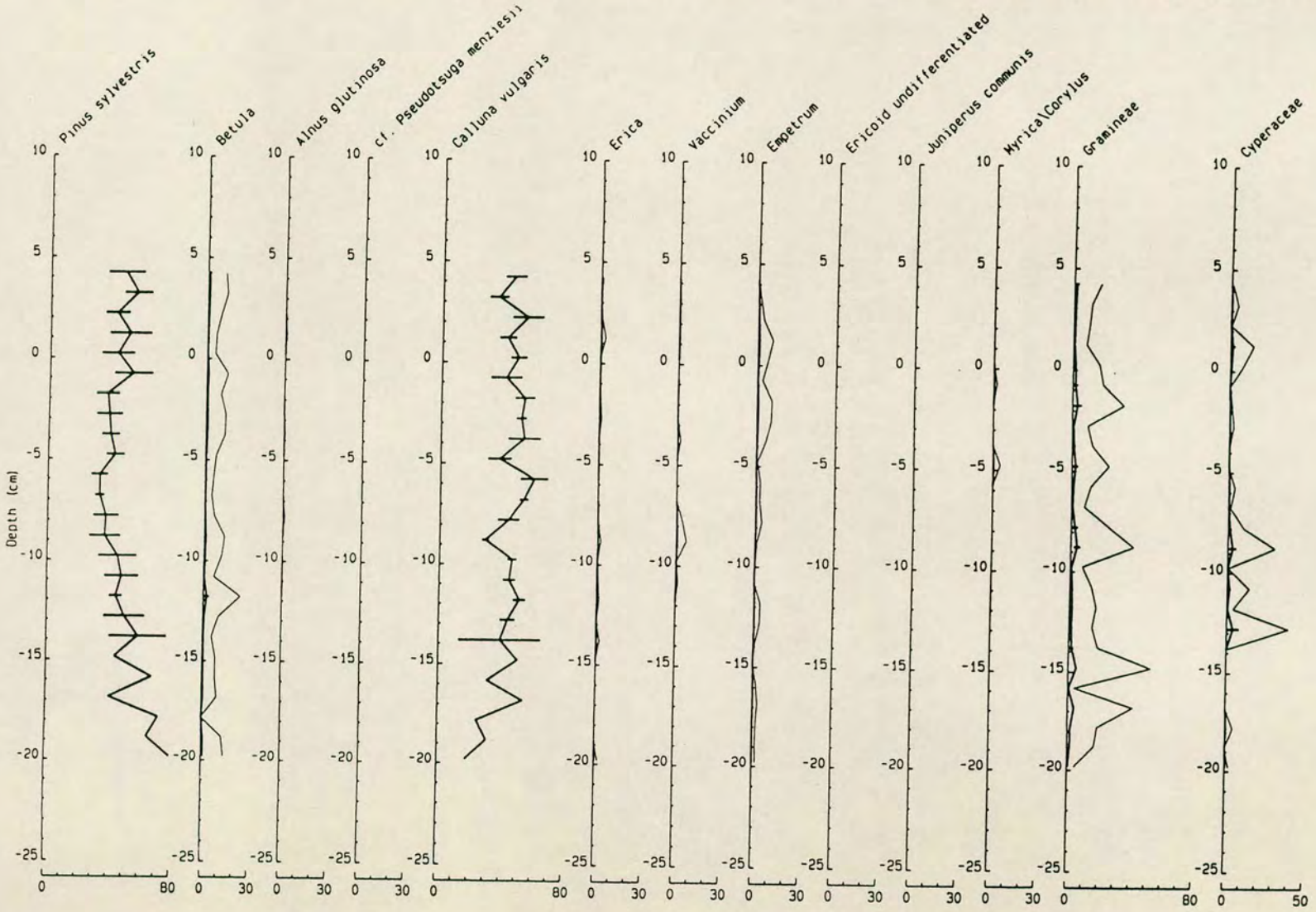
5.3 Palynology Results

5.3.1 Pollen data and diagrams

A total of 26 palynomorphs were described from the Creag Fhiaclach profiles. Of these fifteen were pollen taxa, six were spores, four were testate amoebae (Rhizopoda), one was an algal taxon and the remaining were referred to as unidentified pollen. Fungal spores were not counted as there was some mycelial growth evident before the peat was sub-sampled. This may have affected the distribution of spores. Mean relative pollen diagrams, with standard errors, were constructed for the five replicate cores at each altitude (Figures 5.1 a-f). For compatibility all possible taxa have axes on all diagrams, though not all taxa have curves on all diagrams. Taxa with representation less than five percent are multiplied by a factor of ten and shown as a lighter line. All curves are expressed as percentages of the sum of determinable palynomorphs and are plotted on the same scale. Concentration diagrams were not constructed because of the considerable variation in concentrations. Depths are relative to the base of the litter layer. Depths above this are positive and depths below this are negative. Palynomorphs were well preserved. The only types of damage noted were mechanical ruption or removal of the exine.

As the pollen diagrams are taxonomically poor they were simply plotted as physiognomic groups and not classified according to the shape of curves as is more commonly practised. Pollen diagrams from Creag Fhiaclach were dominated by *Pinus* and *Calluna* pollen. The relative contribution of *Pinus* dropped above the treeline, while the relative proportion of *Calluna* increased slightly above the treeline. Representation of both taxa was variable at the treeline (648 m). *Betula* had slightly higher representation at the two highest altitudes sampled. Of the remaining taxa, Gramineae, Cyperaceae and *Sphagnum* were the most common with no obvious correlation with depth or altitude in their curves. *Pediastrum* was also abundant up to 707 m. Spatial and temporal variation in the remaining taxa was difficult to determine from the pollen diagrams.

Figure 5.1 a: Mean pollen diagram from 606 m at Creag Fhiaclach. Scale on x axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.



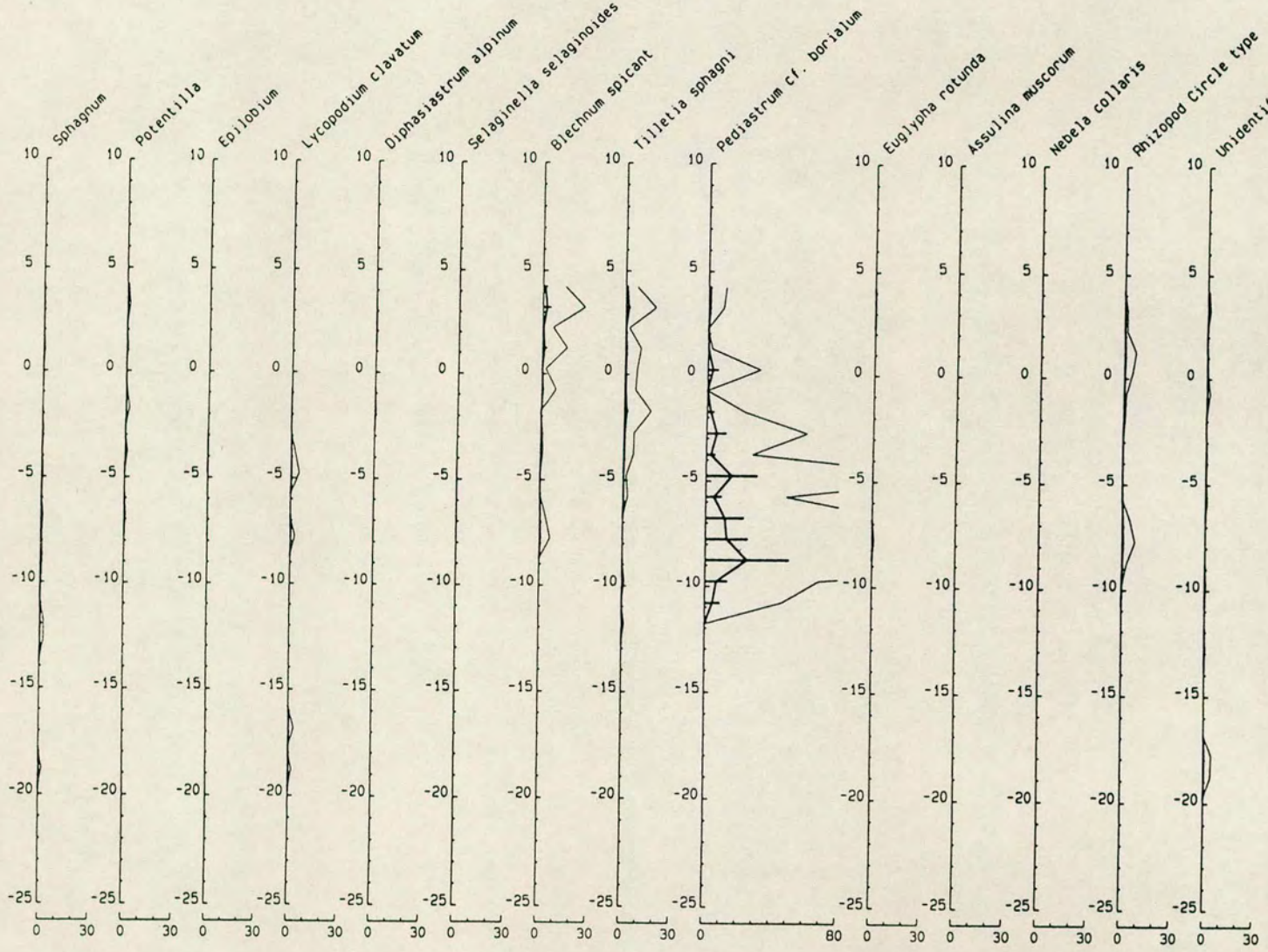
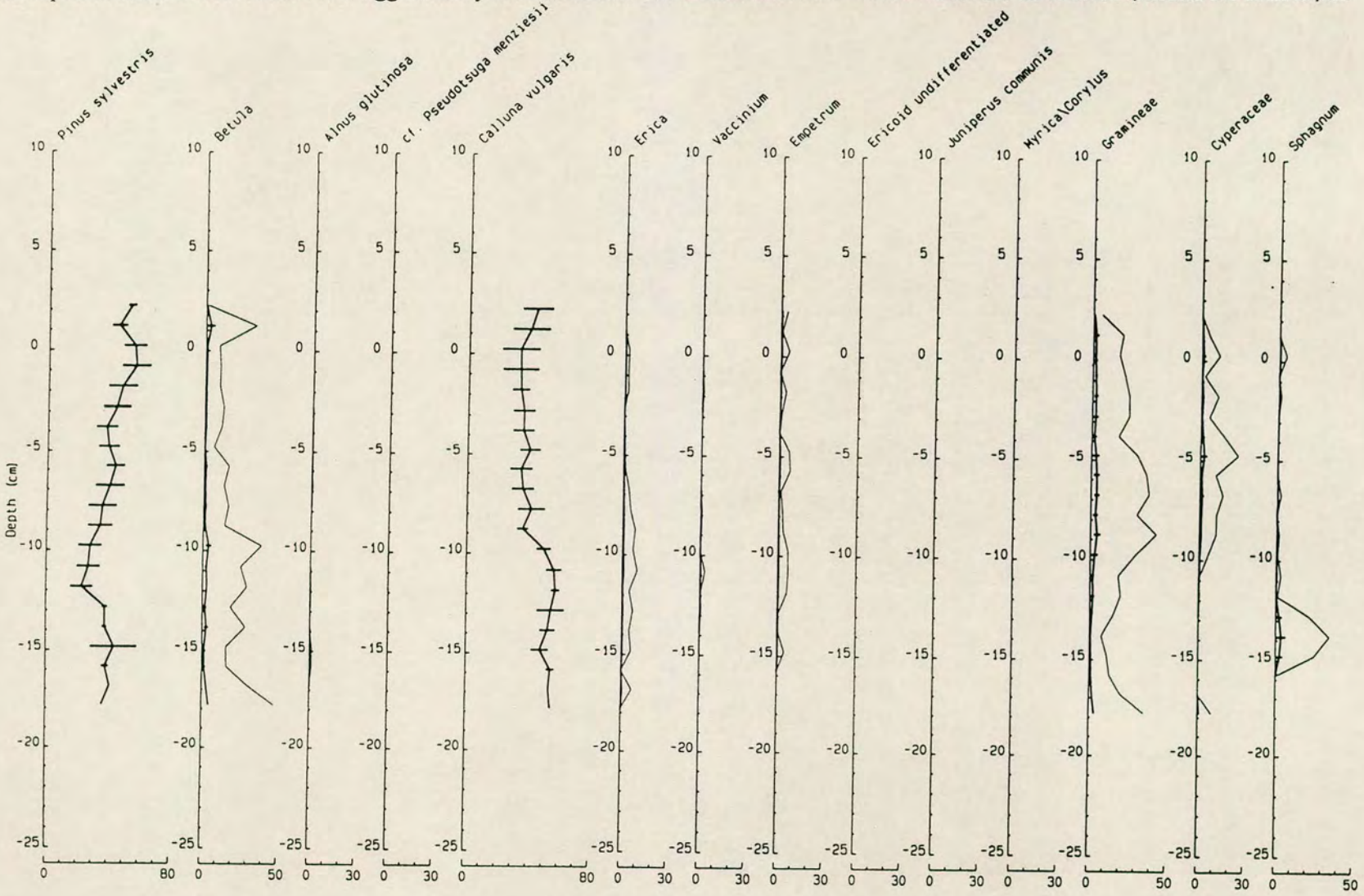
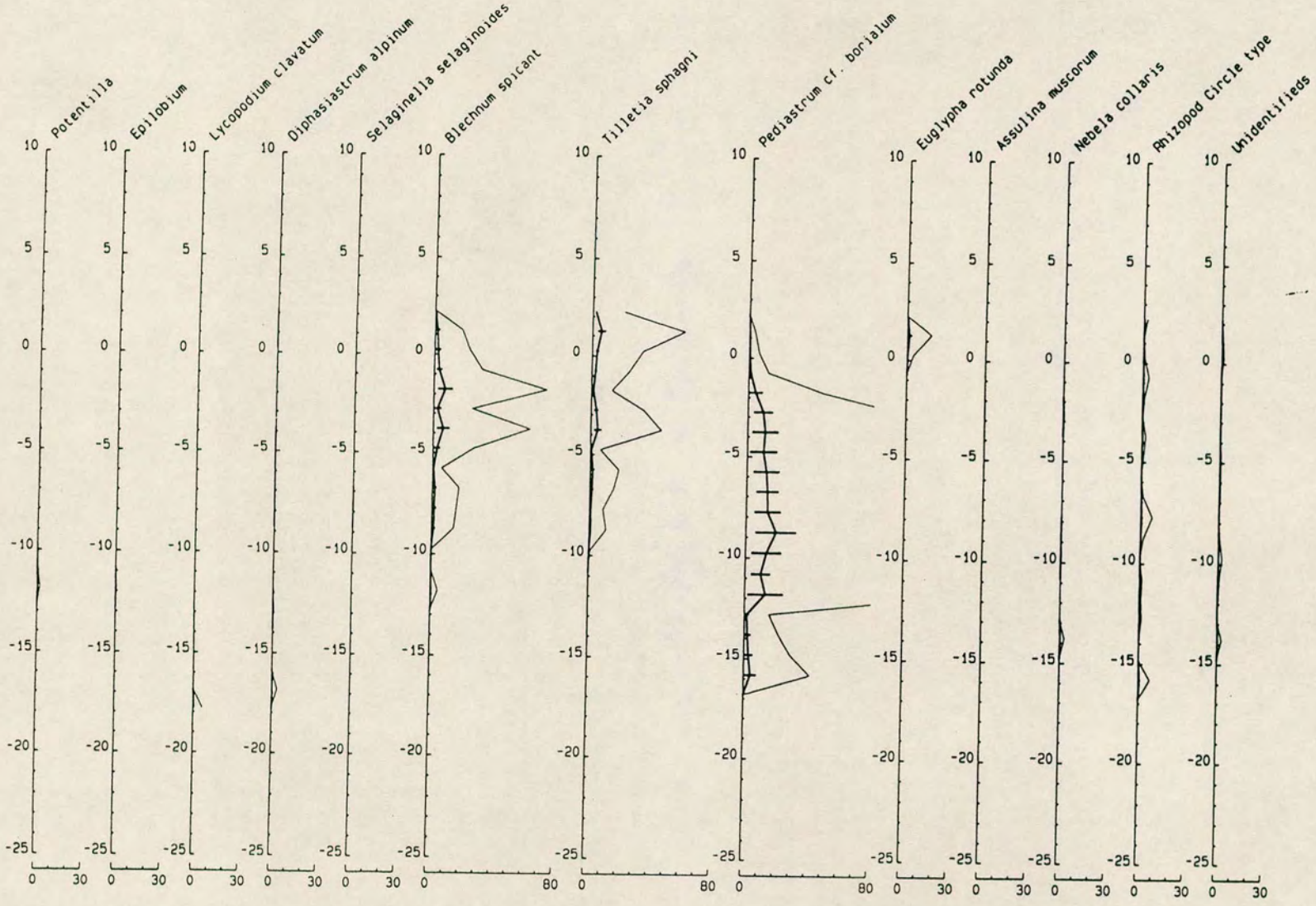

Sphagnum
Potentilla
Epilobium
Lycopodium clavatum
Diphasiastrum alpinum
Selaginella selaginoides
Blechnum spicant
Tilletia sphagni
Pediastrum cf. borialum
Euglypha rotunda
Assulina muscorum
Nebela collaris
Rhizopod Circle type
Unidentifieds
10
5
0
-5
-10
-15
-20
-25
0
30
80

Figure 5.1 b: Mean pollen diagram from 624 m at Creag Fhiaclach. Scale on x axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.




Potentilla
Epilobium
Lycopodium clavatum
Diphasiastrum alpinum
Selaginella selaginoides
Blechnum spicant
Tilletia sphagni
Pediastrum cf. boryalum
Euglypha rotunda
Assulina muscorum
Nebela collaris
Rhizopod Circle type
Unidentifieds
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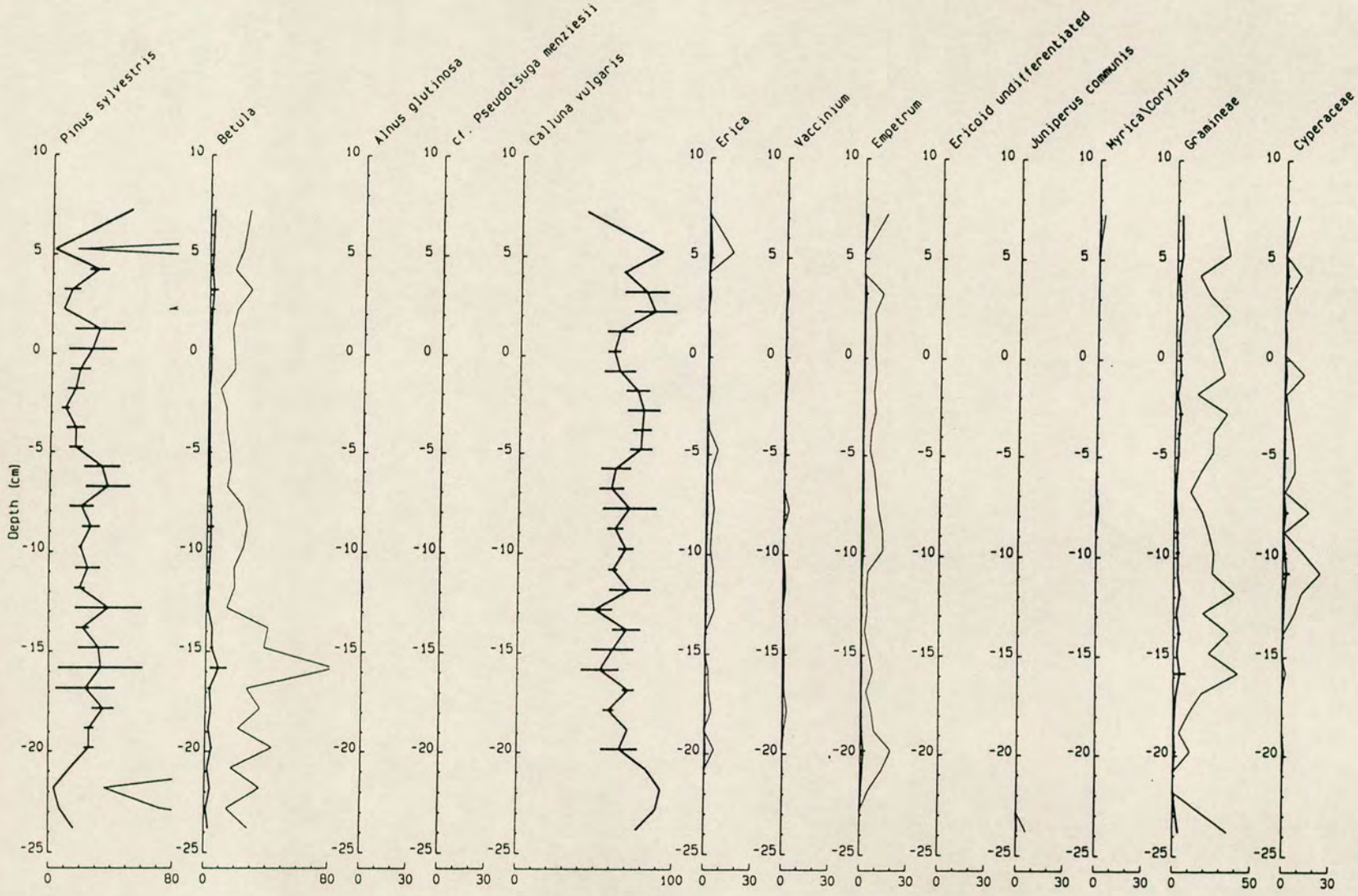
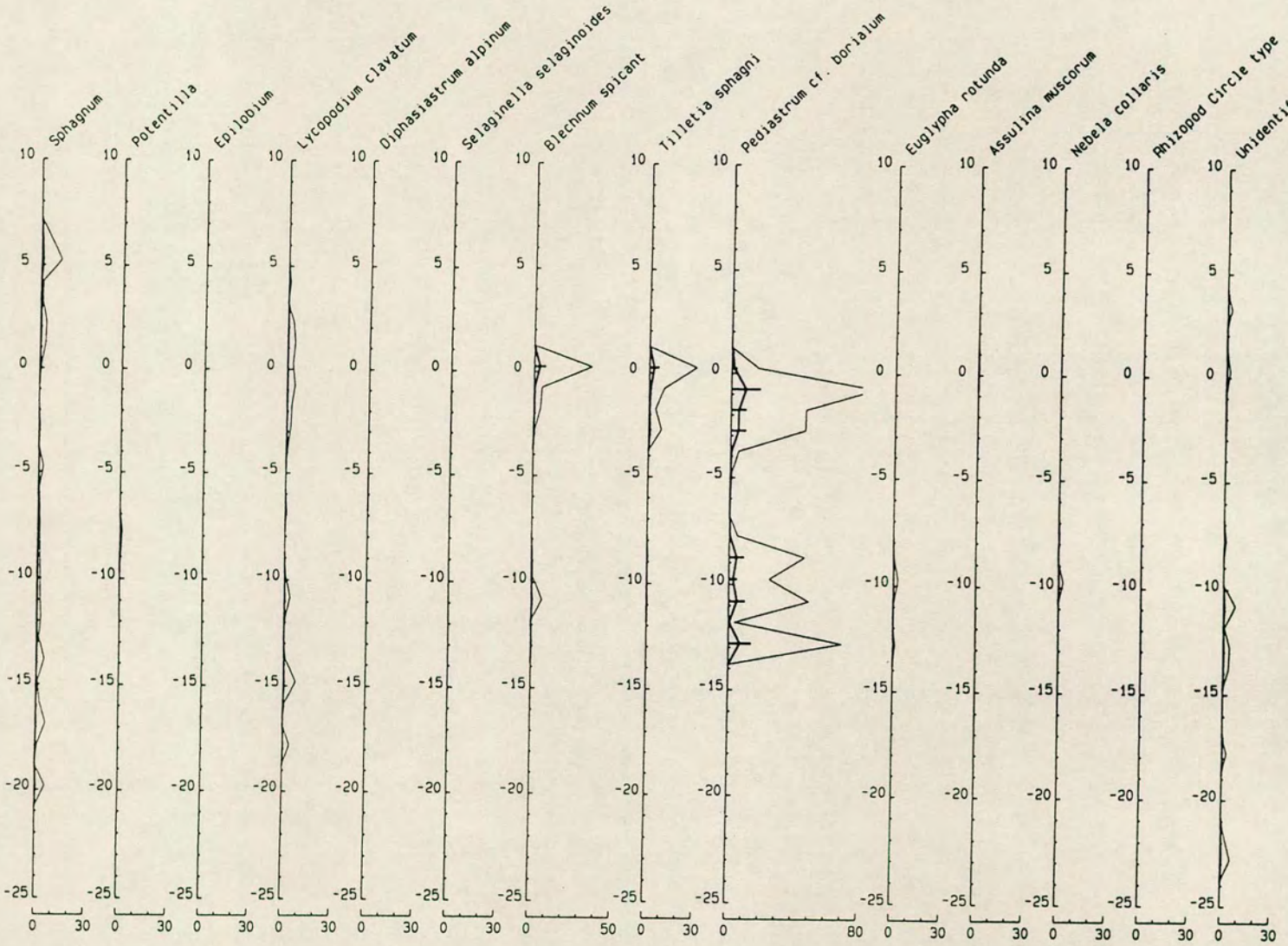
-5
-10
-15
-20
-25
0
30
80

Figure 5.1 c: Mean pollen diagram from 648 m at Creag Fhiaclach. Scale on x axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.

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Potentilla
Epilobium
Lycopodium clavatum
Diphasiastrum alpinum
Selaginella selaginoides
Blechnum spicant
Tilletia sphagni
Pediastrum cf. borialum
Euglypha rotunda
Assulina muscorum
Nebela collaris
Rhizopod Circle type
Unidentifieds
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-5
-10
-15
-20
-25
0
30
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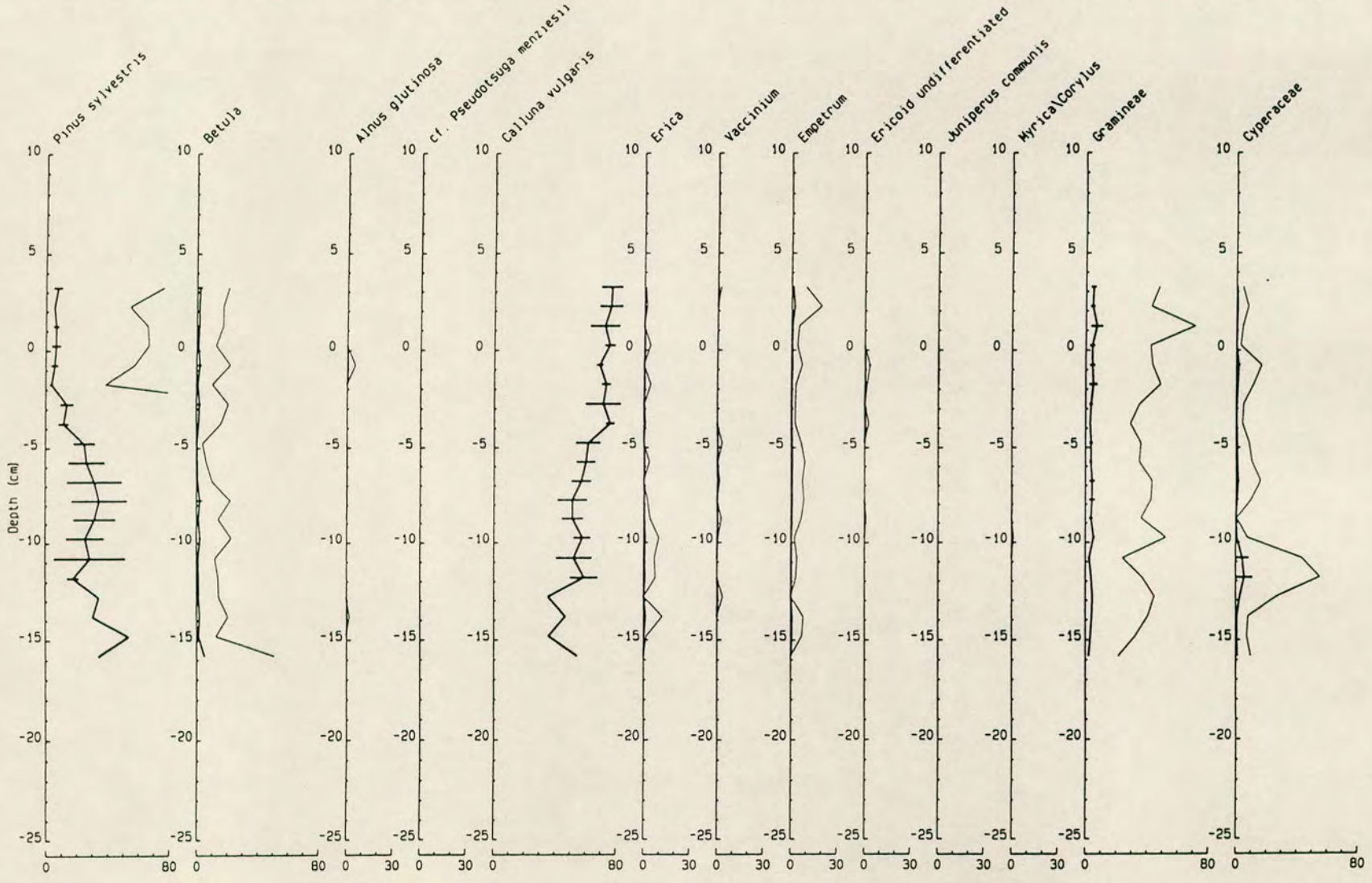
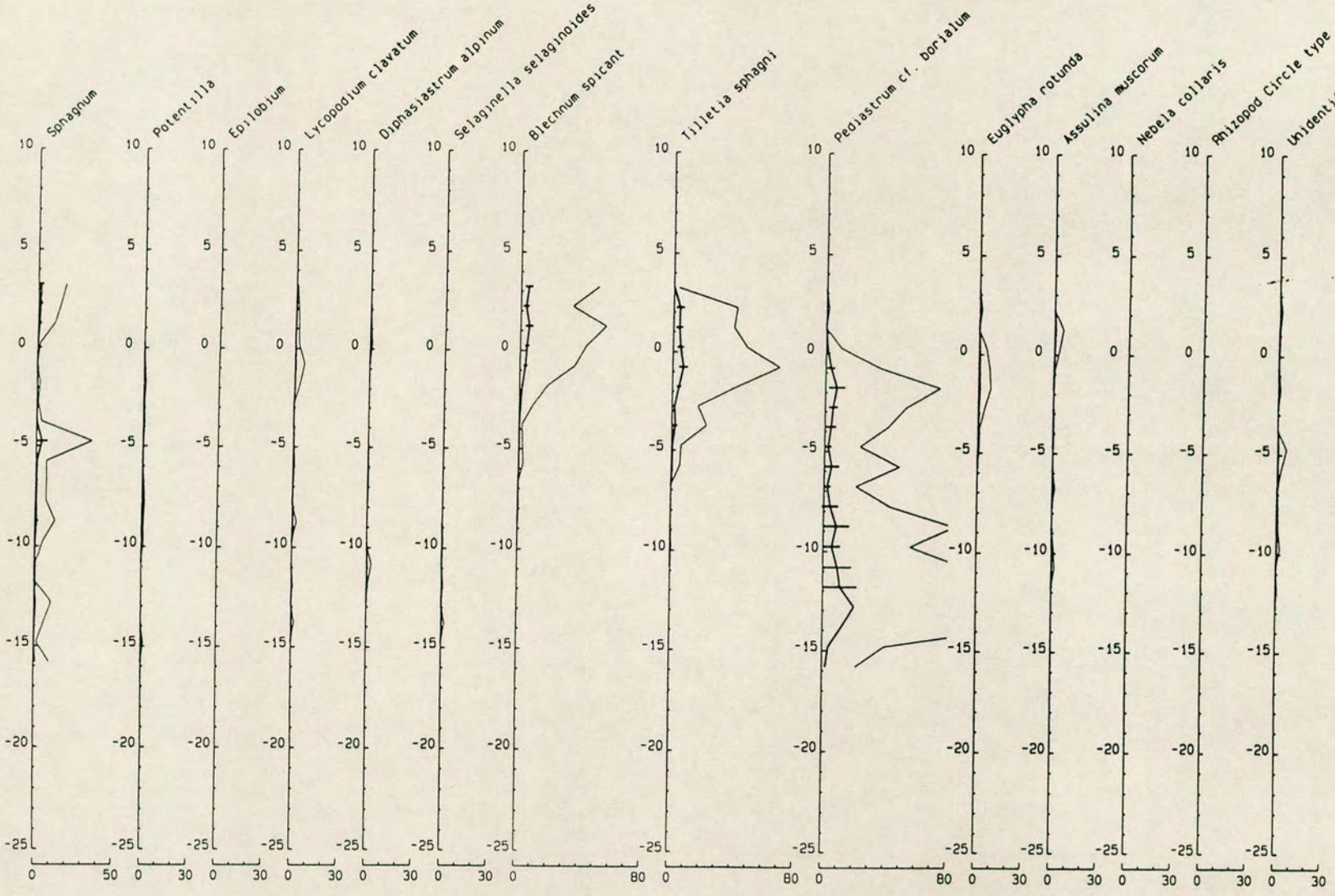
Figure 5.1 d: Mean pollen diagram from 707 m at Creag Fhiaclach. Scale on x axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.

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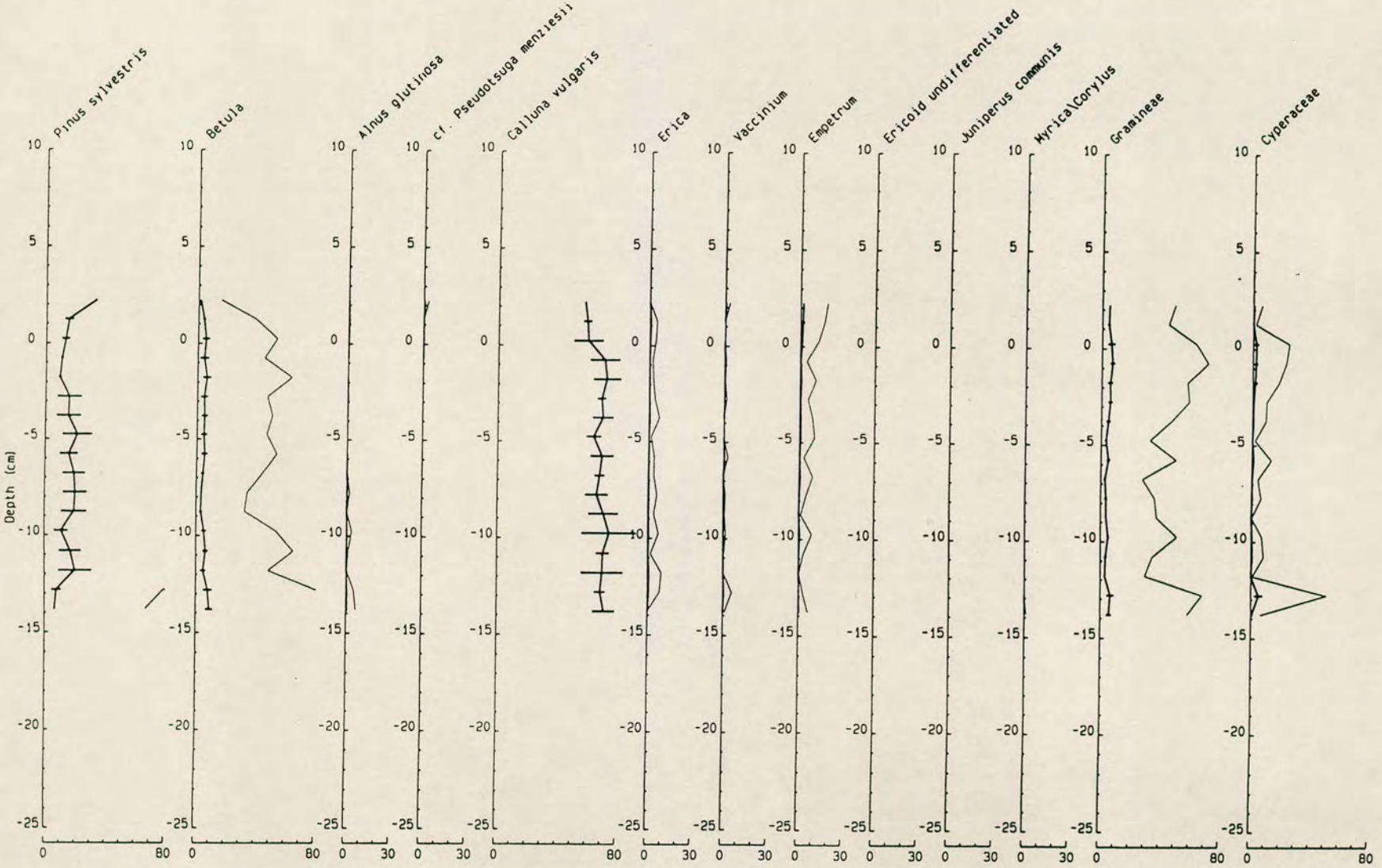
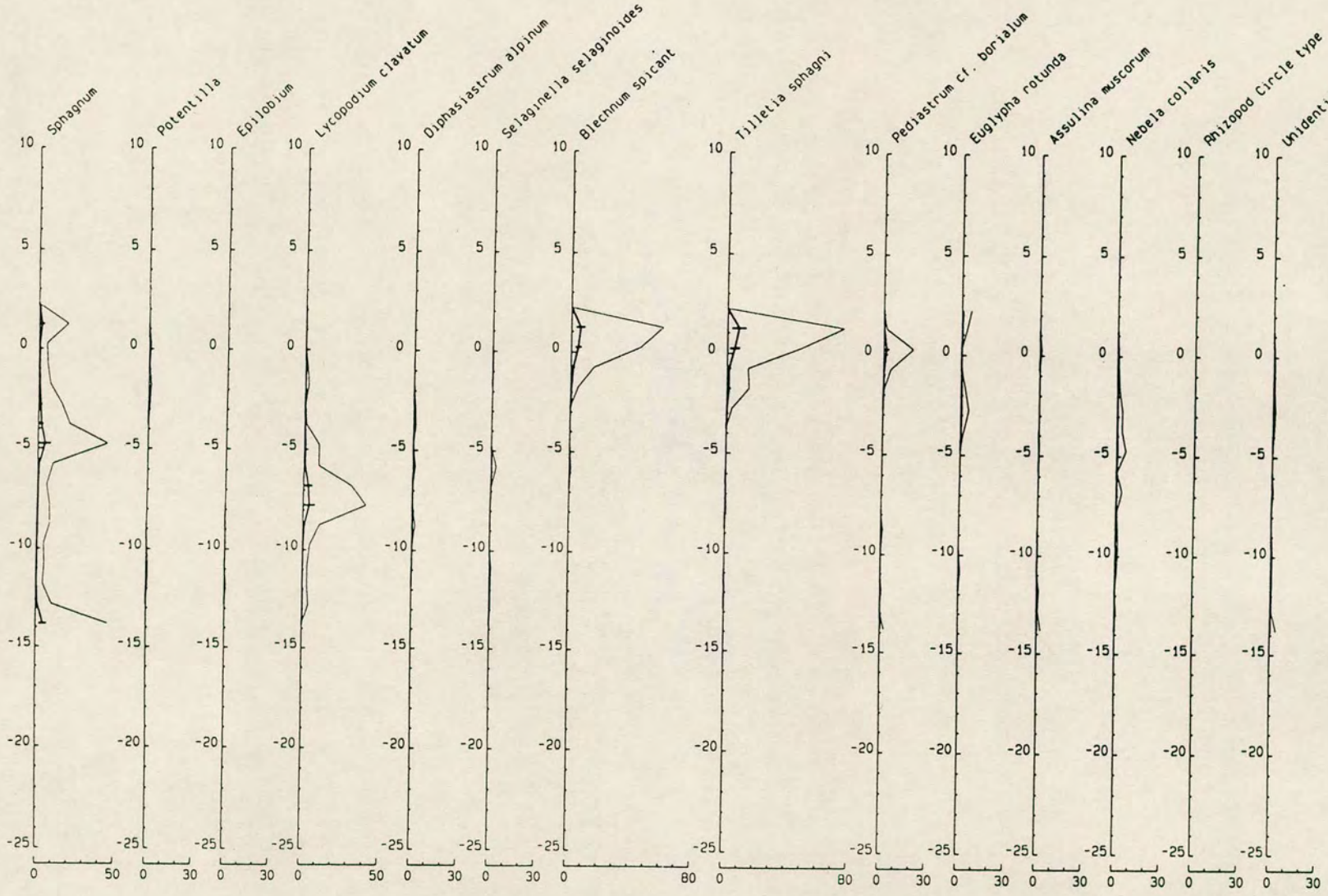
Potentilla
Epilobium
Lycopodium clavatum
Diphasiastrum alpinum
Selaginella selaginoides
Blechnum spicant
Tilletia sphagni
Pediastrum cf. borialum
Euglypha rotunda
Assulina muscorum
Nebela collaris
Rhizopod Circle type
Unidentifieds
10
5
0
-5
-10
-15
-20
-25
0
50
30
80

Figure 5.1 e: Mean pollen diagram from 717 m at Creag Fhiaclach. Scale on x axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.




Sphagnum
Potentilla
Epilobium
Lycopodium clavatum
Diphasiastrum alpinum
Selaginella selaginoides
Blechnum spicant
Tilletia sphagni
Pedastrum cf. borialum
Euglypha rotunda
Assulina muscorum
Nebela collaris
Rhizopod Circle type
Unidentifieds
10
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-5
-10
-15
-20
-25
0
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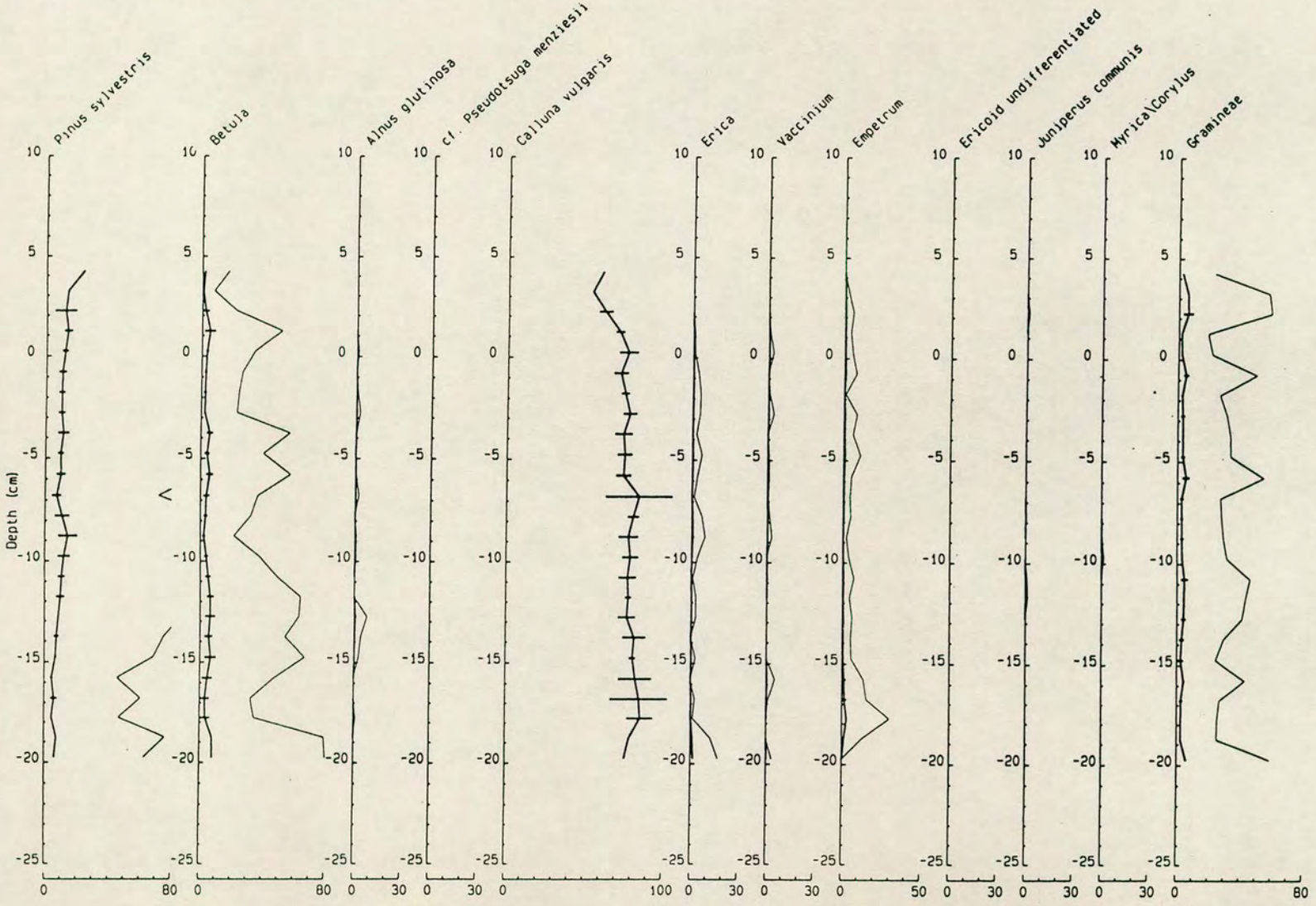
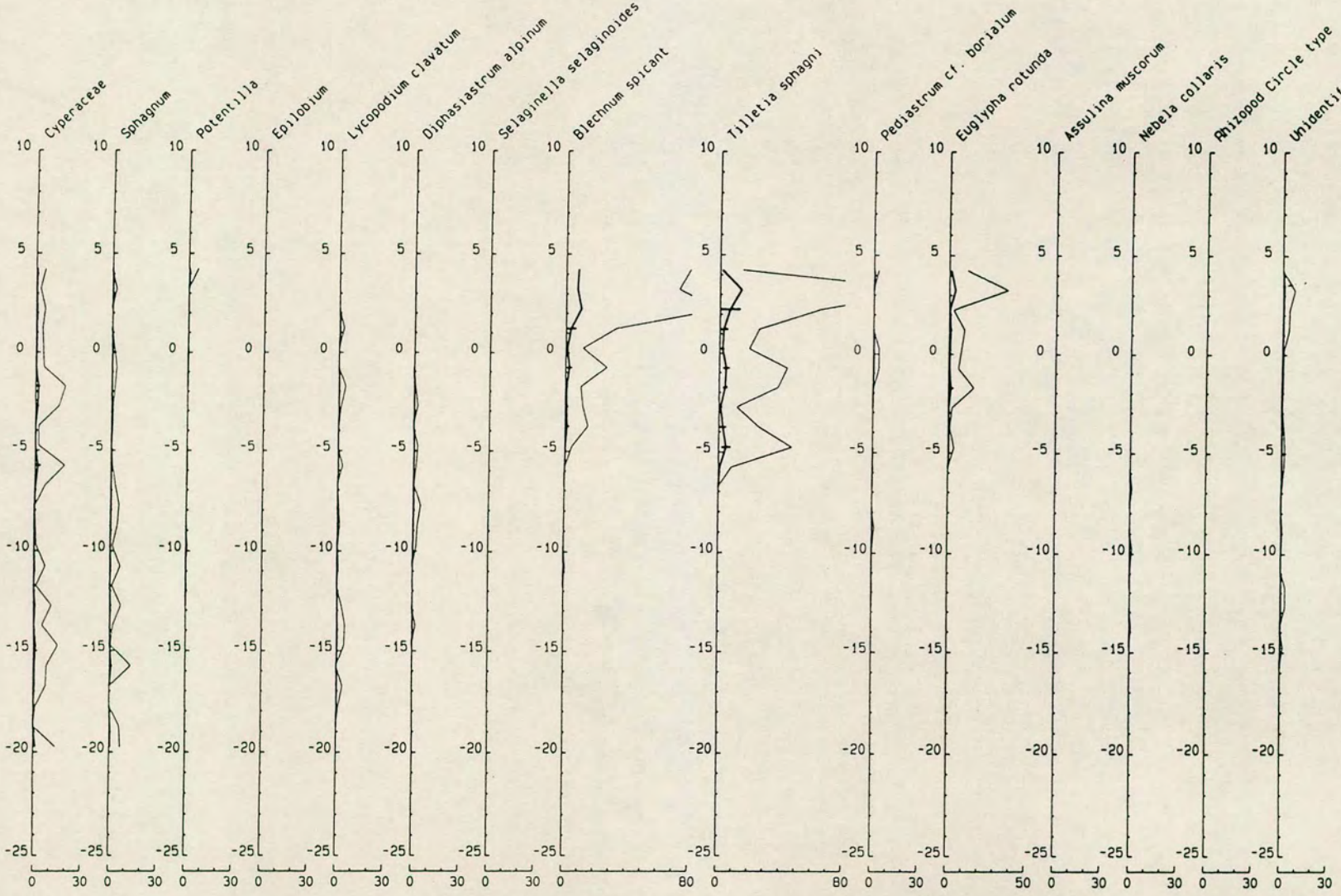
Figure 5.1 f: Mean pollen diagram from 758 m at Creag Fhiaclach. Scale on x axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.




Cyperaceae
Sphagnum
Potentilla
Epilobium
Lycopodium clavatum
Diphasiastrum alpinum
Selaginella selaginoides
Blechnum spicant
Tilletia sphagni
Pediastrum cf. borialum
Euglypha rotunda
Assulina muscorum
Nebela collaris
Rhizopod Circle type
Unidentifieds
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-5
-10
-15
-20
-25
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5.3.2 Reliability of palynological data

Although the number of replicates was determined at each altitude in line with recommendations from section 4.5.2 the idea of replication within depth has not been dealt with. Obviously to replicate counts at each depth within each core would necessitate an unfeasible amount of work. However if the palynological data are to be relied upon and interpreted correctly it is essential that a measure of the variation within depths is estimated. Four pollen samples were identified where there were very large differences in the P*100/(P+C) pollen quotients between adjacent depths. An additional four peat samples were taken from the original cores of each of these depths. Pollen counts were made in the manner given above, and standard deviations of the P*100/(P+C) pollen quotients were calculated (Table 5.1).

Table 5.1: Mean and SD of the P*100/(P+C) pollen quotients within depth increments for individual cores. Mean pollen sums and their associated 95% confidence intervals are given in the final two columns.

Altitude	Core number	Depth	Mean P*100/(P+C)	SD (n=5)	Mean count	95% CI
707 m	rep 4	- 4.75	34.27	3.78	503.8	7.41
606 m	rep 4	- 0.75	73.69	10.13	437.6	19.85
606 m	rep 4	- 4.75	74.95	6.33	441.8	12.41
707 m	rep 5	- 4.75	44.63	3.85	404.2	7.55

The standard deviations and the 95% confidence intervals were acceptably low within each depth. This demonstrates that the pollen quotients were fairly precise estimates and that the observed differences between depths represent real changes.

5.3.3 Distribution of P*100/(P+C) pollen quotients

The differential pollen distribution of the two main pollen producers, *Pinus* and *Calluna* at Creag Fhiaclach allows the present treeline to be detectable in the modern pollen-rain (Chapter 4). Previous treelines should therefore be identifiable from a shift in the P*100/(P+C) pollen quotient at different depths and altitudes in the profile. Figure 5.2 a-f shows quotients plotted against depth for the six altitudes sampled. At 758 m quotients from all depths were below 30%. The quotients the from cores collected within the present day forest (606 m and 624 m) were mostly over 30% at all depths, though a few

Figure 5.2 a-f: P*100/(P+C) pollen quotients from Creag Fhiaclach, Cairngorms. P*100/(P+C) is given on the x axis and the y axis is depth. Depth is shown as positive for the litter and unconsolidated peat and as negative for consolidated peat. Symbols represent □ replicate 1, ◊ replicate 2, Δ replicate 3, ◆ replicate 4 and ■ replicate 5.

Figure 5.2 a: P*100/(P+C) pollen quotient at 606m from Creag Fhiaclach.

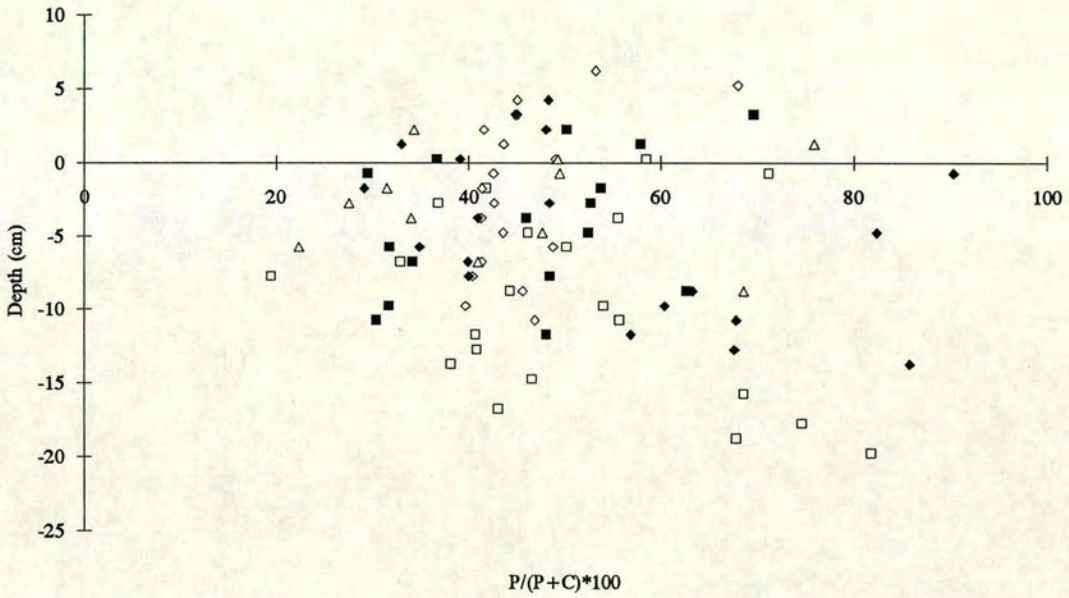


Figure 5.2 b: P*100/(P+C) pollen quotient at 624m from Creag Fhiaclach.

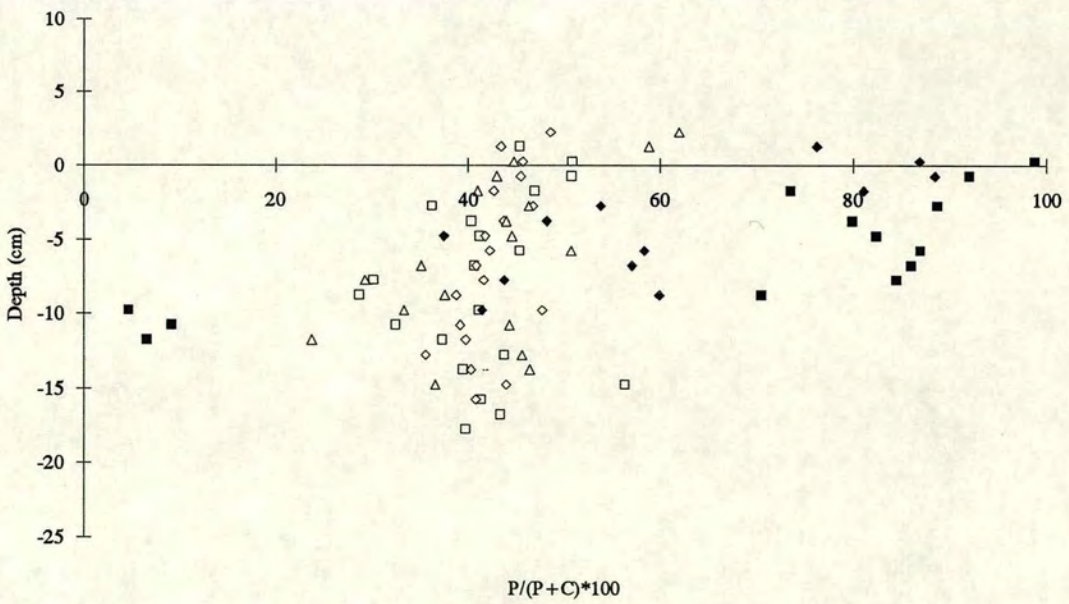


Figure 5.2 c: P*100/(P+C) pollen quotient at the treeline (648 m) at Creag Fhiaclach.

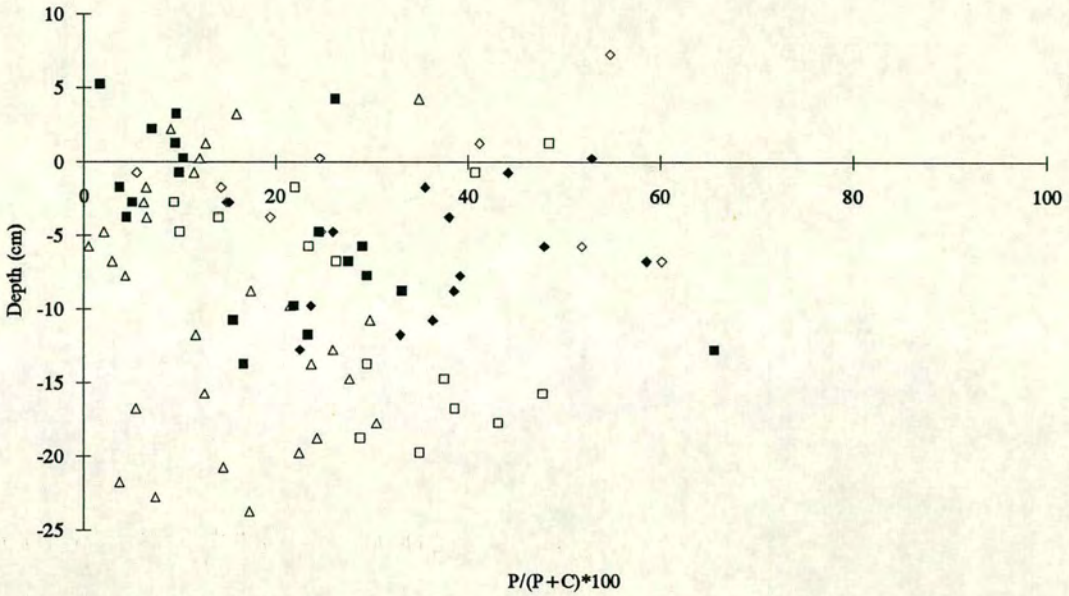


Figure 5.2 d: P*100/(P+C) pollen quotient at 707m from Creag Fhiaclach.

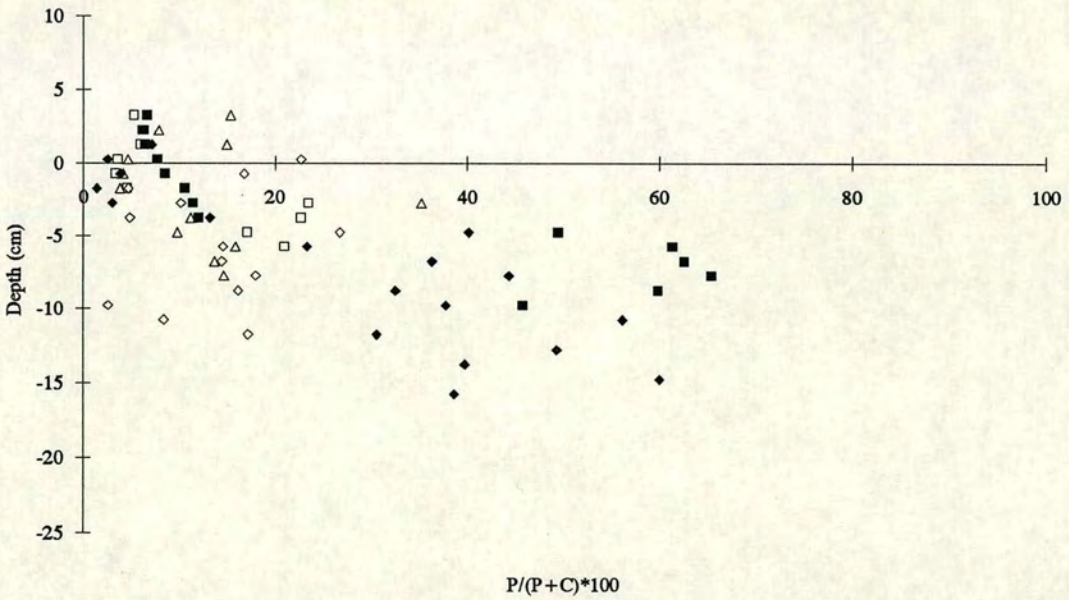


Figure 5.2 e: P*100/(P+C) pollen quotient at 717m from Creag Fhiaclach.

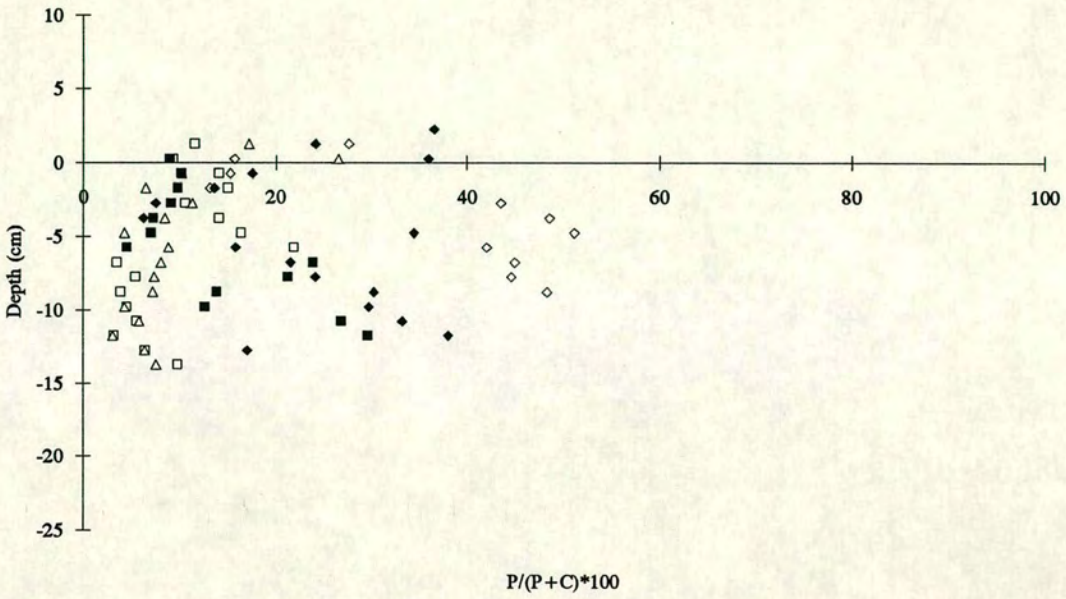
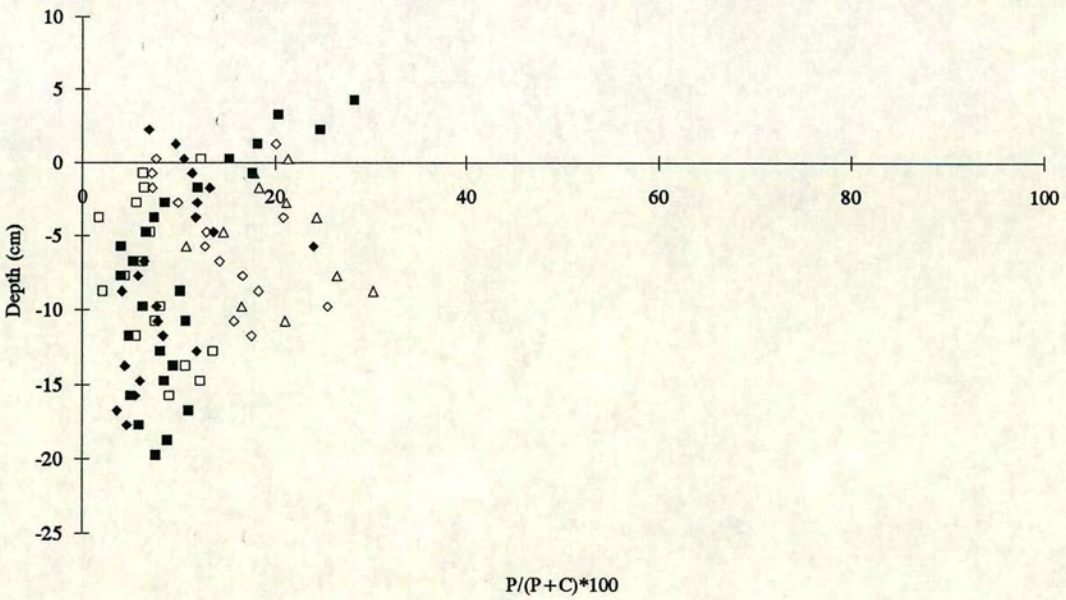


Figure 5.2 f: P*100/(P+C) pollen quotient at 758 m from Creag Fhiaclach.



samples had quotients more typical of heath pollen spectra. All the cores from the treeline had quotients fluctuating widely with depth. These fluctuations showed no synchrony with depth. At 707 m quotients in replicates 1 - 3 were all low. The tops of replicate cores 4 and 5 were also low until -3.75 cm. Below this depth the quotients are higher in *Pinus* representation in both cores. At 717 m replicate 4 also has quotients in the 40-50% range at depths below -3.75 cm. Replicate two shows consistently higher quotients between -9.75 cm and -12.75 cm depths, but these are absent at 707 m and are not consistently high between depths sampled at 717 m.

5.3.4 Discriminant Analysis

Solomon & Silkworth (1986) described how pollen in a montane environment was deposited according to a step-wise function. A selected pollen taxon from one vegetation belt was quickly attenuated in the vegetation belts immediately above and below and in other belts was constant. This had implications for interpreting sub-fossil pollen assemblages in that, once outside the immediate vegetation belts, representation of the pollen taxon gives no indication of the direction of the vegetation in which it originated, *i.e.*, it could equally be derived from a higher or lower vegetation belt. Indicator species in the minor taxa of pollen assemblages was used by Spear (1989) to determine whether any particular sample with high AP was from above or below the treeline. Pollen quotients in the modern pollen-rain study had a high representation of *Pinus* in the forest and in high altitude heath. Distribution patterns of minor taxa that may be able to distinguish the pollen assemblage as forest or high altitude heath were investigated using discriminant function analysis.

Pollen data from the surface sample in each core were used to determine the discriminant function that best separates forest from heath pollen spectra. The discriminant function was based on the surface samples with all sub-surface samples declared as unknown. Initially, three groups were used for discrimination on the basis of vegetation cover. These were forest, treeline and heath. The inclusion of a treeline class caused the misclassification of six samples. Sub-surface samples from cores within the forest were assigned to either treeline and forest classes without any particular patterns. The same was true of cores at the treeline, but here some heath classes also occurred. These results indicate that treeline samples are not reliably distinguishable from forest. Therefore in the

subsequent analyses treeline samples were classifed as forest. The stepwise discriminant function analysis routine of BMDP (Dixon, 1985) was run with the default F-to-enter and F-to-remove values of 4 and 3.996 respectively. This allowed only a single taxon, *Pinus* to contribute to the discriminant function. However, two of the surface samples remained misclassified. Changing the default F-to-enter to 3 and F-to-remove to 2.996 allowed a further four taxa to contribute to the classification and no surface samples were misclassified. BMDP also has a facility for limiting the number of steps as well as determining the minimum F-to-enter or remove. Using this facility the minimum number of taxa required to prevent misclassification of the surface samples was found to be five.

At step 0, before any variable was entered into the discriminant function, the two variables with the highest F-to-enter were *Pinus* (36.77) and *Calluna* (19.56) (full details of steps 0-5 are given in Appendix IV). When *Pinus* was entered in step 1 the F-to-enter value of *Calluna* dropped to 0.78. *Pinus* and *Calluna* can be seen to share the same information content. Step 2 was the inclusion of *Betula* that increased the F-to-enter values of the two rhizopods *Euglypha rotunda* and circular morph. Circular morph was entered at step 3. Step 4 identified *Diphasiastrum alpinum* as having a significant contribution. Emphasis shifted back to the Ericaceous species at step 5 when *Erica* was entered. Summary tables of the output of the discriminant analysis on the basis of these five taxa are shown in Tables 5.2 to 5.5.

Table 5.2: Summary of results from the discriminant analysis. The F-to-enter is the F-statistic corresponding to the ANOVA on the residuals of the variable. The U-statistic (Wilks' Lambda) is a multivariate analysis of variance that tests the equality of the group means for the variable(s) in question. Wilks' Lambda can be directly compared to the F distribution by conversion to an approximate F-statistic. This allows a determination of the significance of a variable in delineating the groups. Significance levels are given in the last column (NS = non-significant, * $P<0.05$, ** $P<0.01$, *** $P<0.001$).

Step	Variable entered	F - ratio	U-statistic	Approximate F-statistic	df		Significance
1	*Pinus*	36.8	0.43	36.8	1	28	***
2	*Betula*	3.5	0.38	21.8	2	27	***
3	Circular morph	3.5	0.34	17.1	3	26	***
4	*D. alpinum*	3.1	0.30	14.6	4	25	***
5	*Erica*	6.3	0.24	15.4	5	24	***

Table 5.3: The final discriminant function on the basis of five steps. The relevant variable group for each sample is simply multiplied by the appropriate function and the constant value is added. This is calculated for both heath and forest functions. The sample was then classified into the group that gave the largest numerical value.

Variable group	Heath	Forest
Pinus	4.30	28.79
Birch	144.57	-20.42
Circular morph	-31.33	468.34
D. alpinum	712.53	-1125.99
Erica	250.67	-206.51
Constant	-3.42	-7.54

Table 5.4: The classification matrix shows the number of cases classified into each group and the percentage of correct classifications.

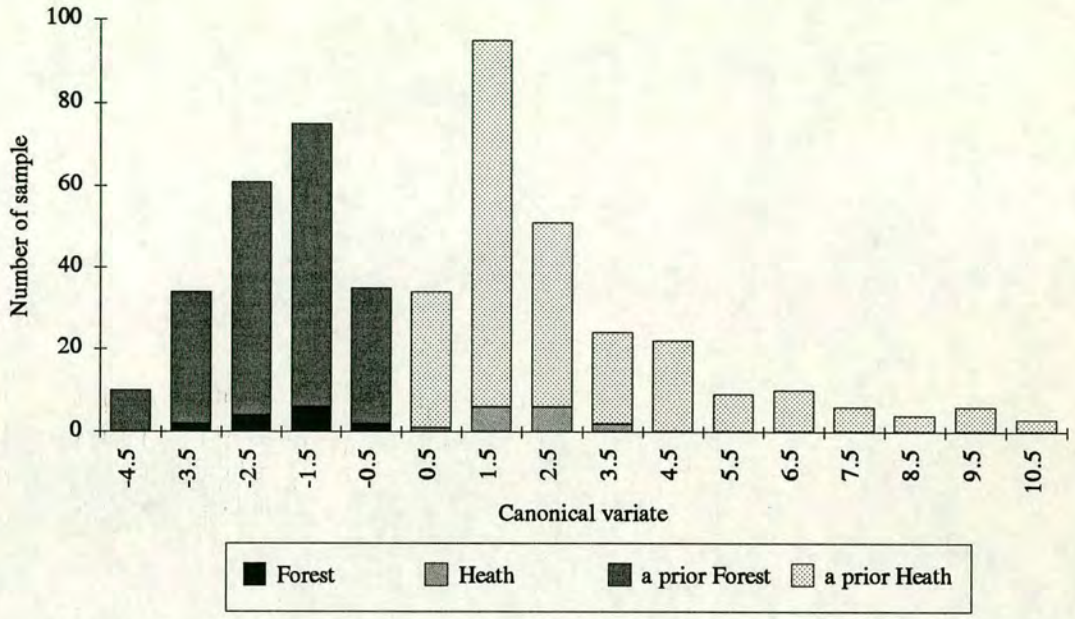
Original	Classification		
Group	Percent correct	Number of cases	
		Heath	Forest
Heath	100	15	0
Forest	100	0	15
Unknown		249	202

Table 5.5: The jack-knifed classification matrix shows the same information as the classification matrix, but on the basis that each case was classified using the classification function computed from all cases, except the case being classified.

Original	Classification		
Group	Percent correct	Number of cases	
		Heath	Forest
Heath	93.3	14	1
Forest	86.7	2	13
Unknown		249	202

The canonical variables at group means were 1.7 for heath and -1.7 for forest samples. The canonical variable for the unknown group mean was 0.6. The distribution of canonical variables for all cases are displayed in Figure 5.3.

Figure 5.3: Distribution of the canonical variables for all cases. The discriminant index is the mid point between the canonical variables for the group means and in this case equates to zero. Therefore samples with positive canonical variables are classed as heath and those with negative variables are forest.



Final classification of all cases are displayed in Figure 5.4. Depth is on the y-axis and the x-axis is the canonical variable. At 758 m most pollen spectra were classified as heath spectra by the discriminant function. One sample from replicate two and four samples from replicate three were classified as forest samples. Most of the pollen spectra at this elevation had widely scattered positive values of the canonical variable. Only replicate four has a tight distribution of the canonical variable. Cores from the two lowest altitudes consisted predominantly of forest pollen spectra. Heath spectra occurred in all cores, except replicate two at 606 m. The distribution of the heath spectra are erratic. All replicates at the treeline and at 707 m had a mixture of heath and forest pollen spectra. Overall samples tended to be clustered around zero. Replicate five from a depth of -4.75 cm at 707 m was consistently classified as forest type. Most spectra in replicate four beneath -4.75 cm were also forest types. The exceptions occur at -7.75, -8.75 and the bottom sample. Forest samples from the other replicates occurred erratically.

Figures 5.4 a-f: Classification of pollen spectra from Creag Fhiaclach on the basis of the discriminant function from surface samples. The canonical variate for each sample is plotted against depth. Depth is shown as positive for the litter and unconsolidated peat and as negative for consolidated peat. Symbols represent □ replicate 1, Δ replicate 2, O replicate 3, □ replicate 4, ◊ replicate 5. Blank symbols represent forest type and filled symbols represent heath type, except for replicate four where forest types are represented by a cross and heath types by a larger filled box.

Figure 5.4 a: Classification of pollen spectra at 606m from Creag Fhiaclach.

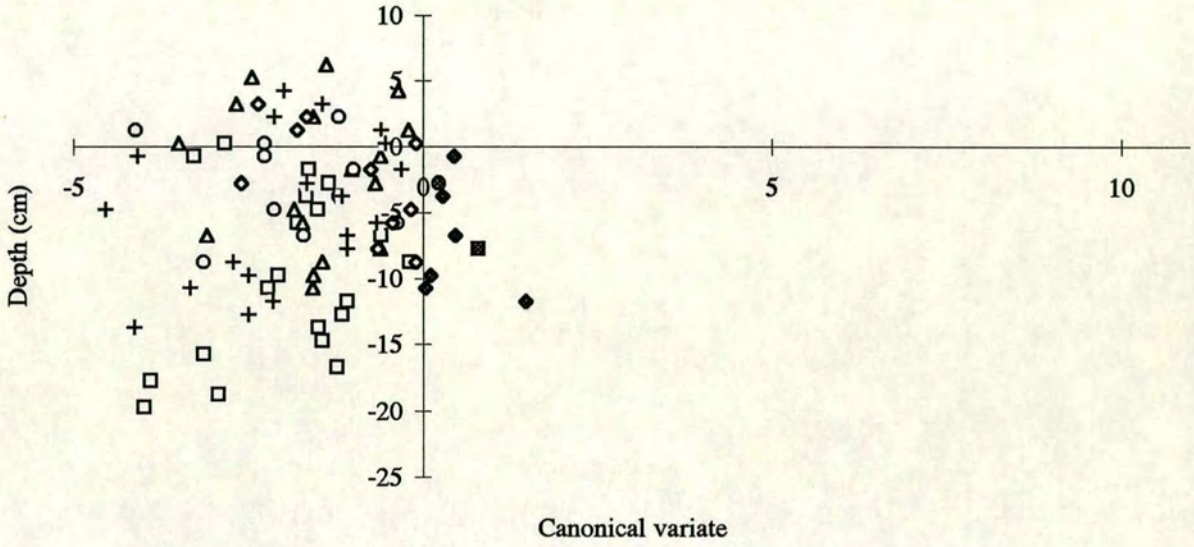


Figure 5.4 b: Classification of pollen spectra at 624m from Creag Fhiaclach.

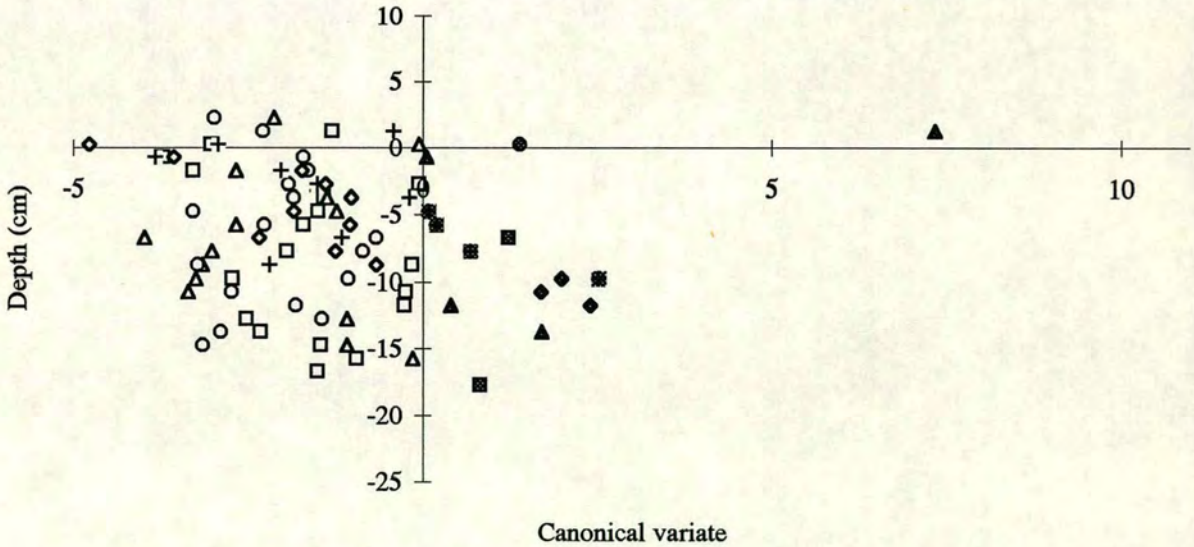


Figure 5.4 c: Classification of pollen spectra at the treeline (648 m) at Creag Fhiaclach.

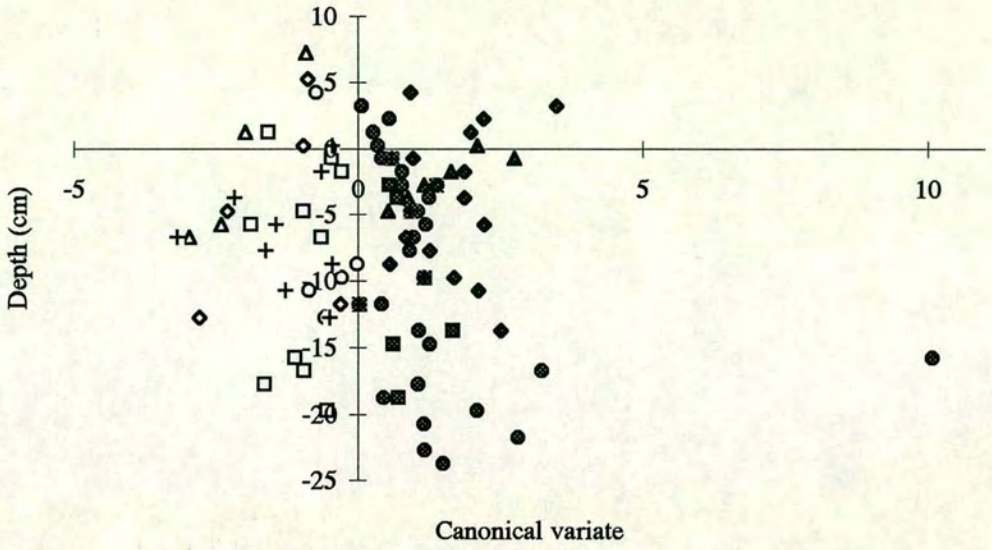


Figure 5.4 d: Classification of pollen spectra at 707m from Creag Fhiaclach.

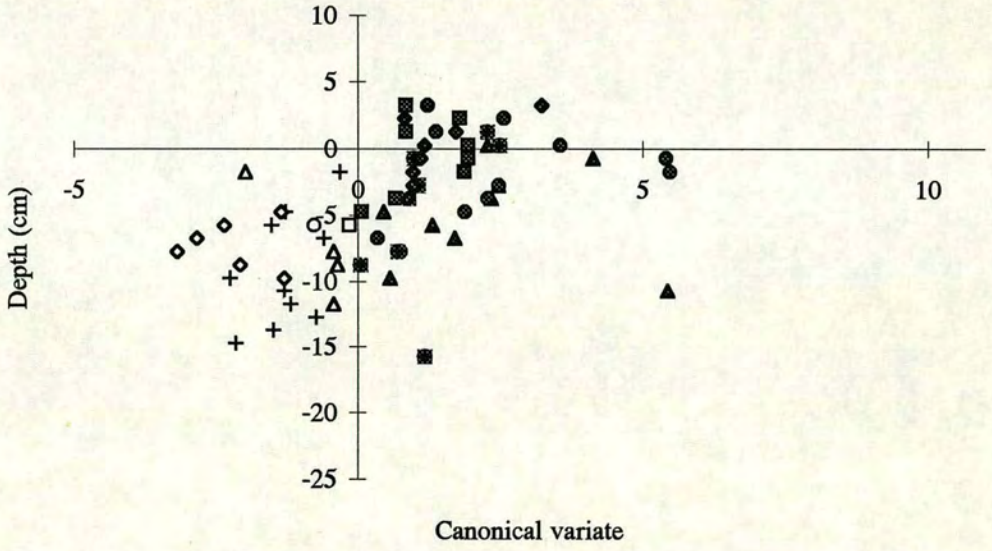


Figure 5.4 e: Classification of pollen spectra at 717m from Creag Fhiaclach.

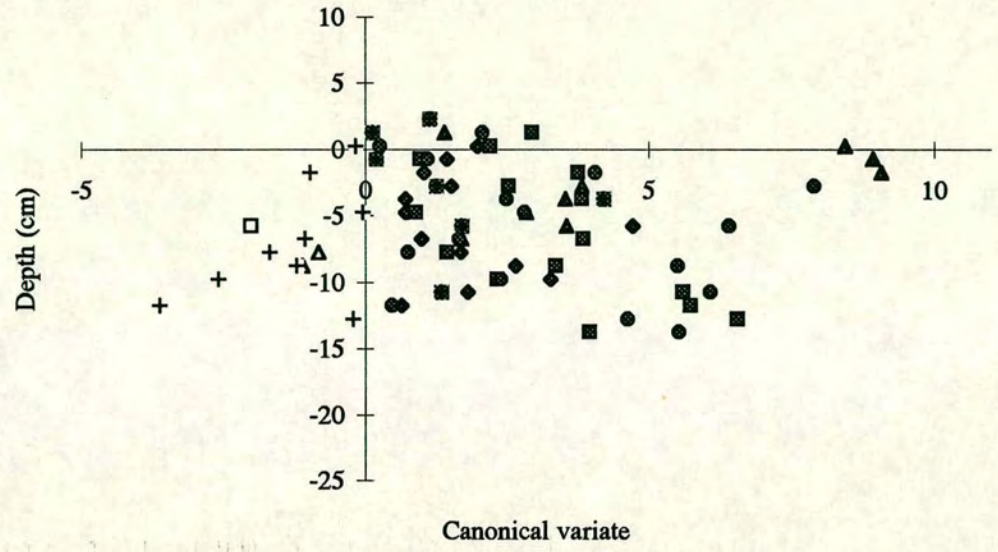
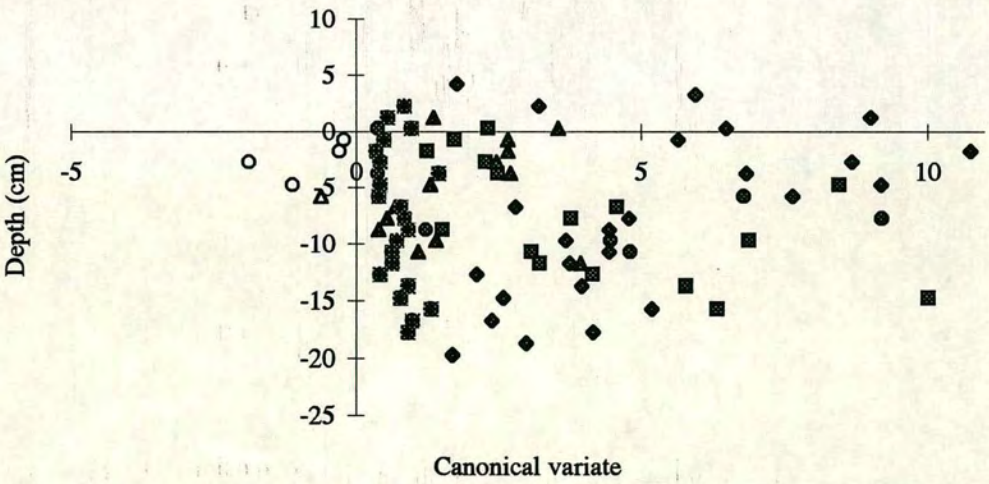


Figure 5.4 f Classification of pollen spectra at 758 m from Creag Fhiaclach.



In addition to a listing of the classification of the unknown cases, BMDP (Dixon, 1985) also gives the Mahnalobis D^2 distances for each case from the group means for the predefined forest and heath samples. Outliers can be detected using the D^2 distances. D^2 from any case to a group mean follows the chi-square distribution. The degrees of freedom are equal to the number of steps in the function; in this case 5. The 1% and 0.1% significance levels at 5 degrees of freedom are 11.07 and 15.09 respectively. Therefore, if the D^2 distance is above 15.09 from both group means the sample can be regarded as an outlier. The spatial and temporal distribution of outliers is shown in Figure 5.5. Outliers occur at all altitudes. All spectra with the canonical variable over 5.0 were outliers. The majority of these were at 717 and 758 m.

5.3.5 Principal components analysis

The first axis of the PCA was dominated by rhizopod taxa and *Pinus* at the positive end with *Calluna* and *Betula* at the negative end (Table 5.6). The first axis explained 27.5% of the variance (Table 5.7). The second axis separates *Pinus* from the rhizopod taxa and explains 19.5% of the variation. *Calluna* has an eigenvector loading of nearly zero on both the second and third axes. The positive end of axis three was dominated by rhizopod taxa. *Nebela collaris* and *Betula* characterised the negative end. Axis four consisted of *Betula*, Gramineae and *Pinus* at the negative end with *Calluna* at the positive end.

The first two PCA axes were plotted as a site-species biplot (Figure 5.6). The length of the arrows in the biplot are indicative of the influence of the species that it represents (Jongman *et al.*, 1987). The directions of arrows relative to one another indicate the correlations between species. Arrows in opposite directions in the plane of the ordination diagram represent negatively correlated species and those in the same direction are positively correlated. Short arrows indicate a lack of correlation in the plane of the ordination diagram. The longest species gradient in the biplot was the Gramineae-*Pinus* gradient. The second longest gradient runs at right angles to this and was a rhizopod/Cyperaceae community to rare taxa gradient. Many of the site scores were clustered along the Gramineae - *Pinus* gradient with some scattering in the rhizopod-Cyperaceae direction. Down-weighting the rare taxa that predominated on axis two had very little influence on the biplot.

Figures 5.5 a-f: Distribution of outliers from the discriminant function analysis on pollen spectra from Creag Fhiaclach. The canonical variate for each sample is plotted against depth. Depth is shown as positive for the litter and unconsolidated peat and as negative for consolidated peat. Open boxes represent outliers.

Figure 5.5 a: Distribution of outliers at 606m from Creag Fhiaclach.

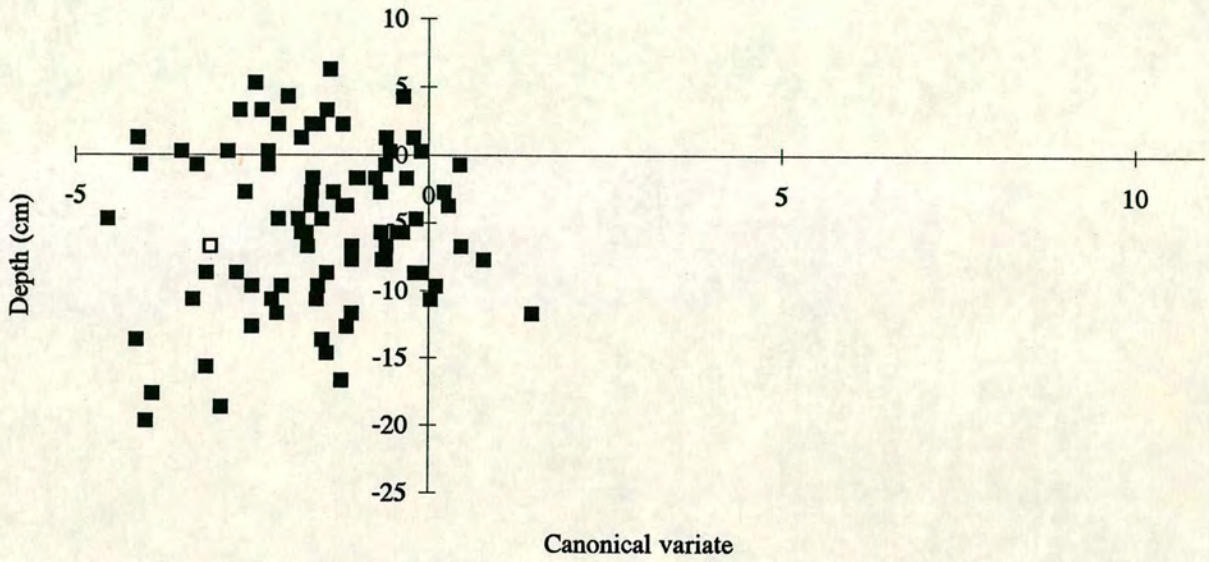


Figure 5.5 b: Distribution of outliers at 624m from Creag Fhiaclach.

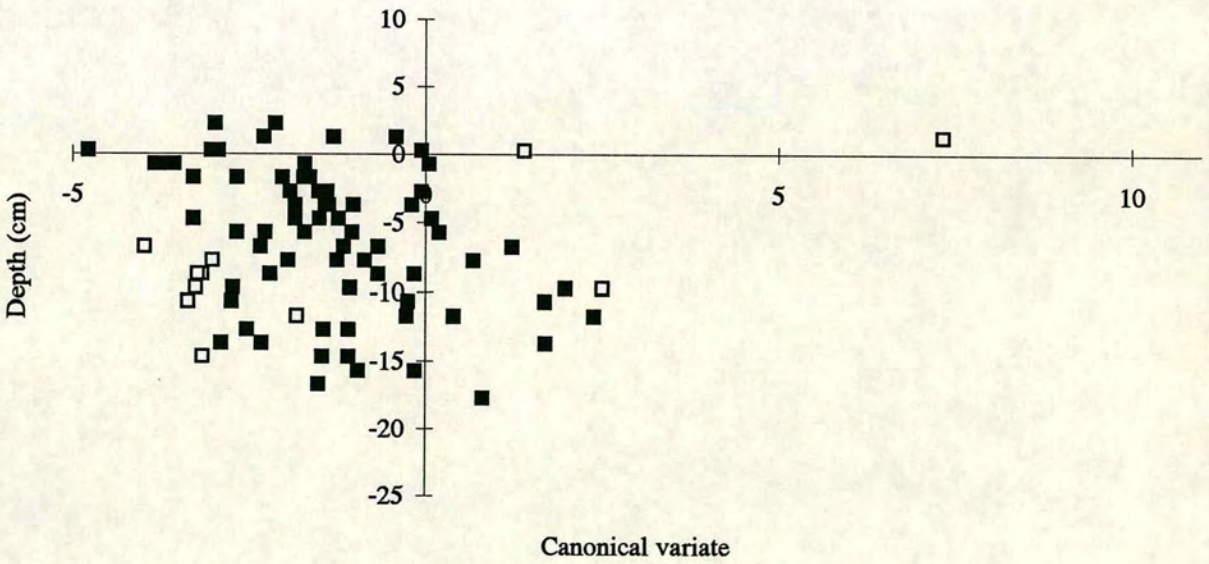


Figure 5.5 c: Distribution of outliers at the treeline (648 m) at Creag Fhiaclach.

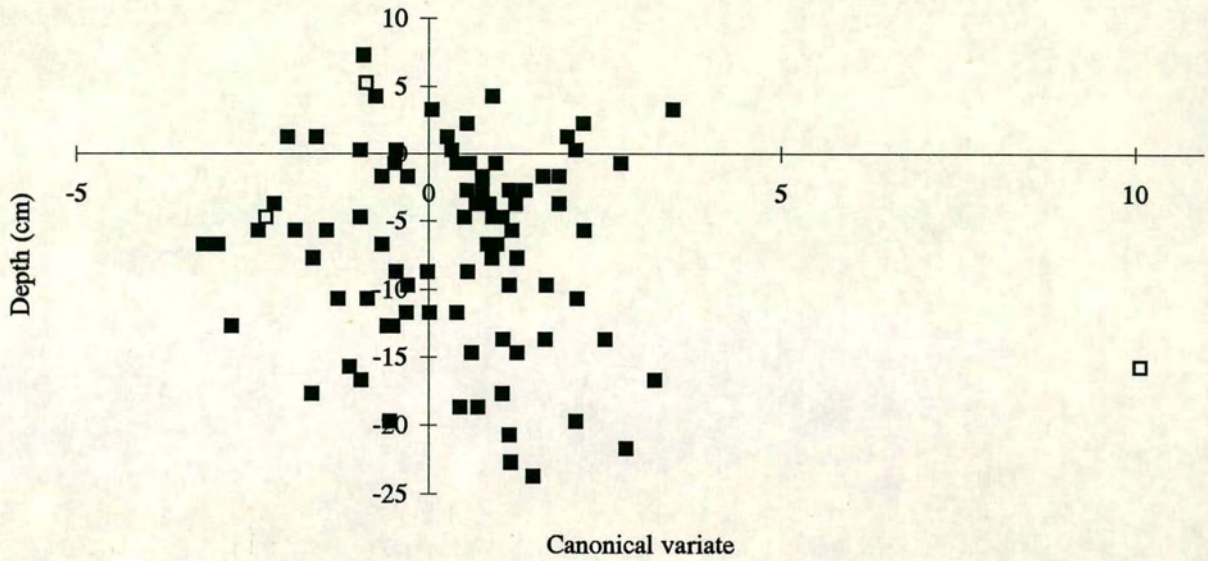


Figure 5.5 d: Distribution of outliers at 707m from Creag Fhiaclach.

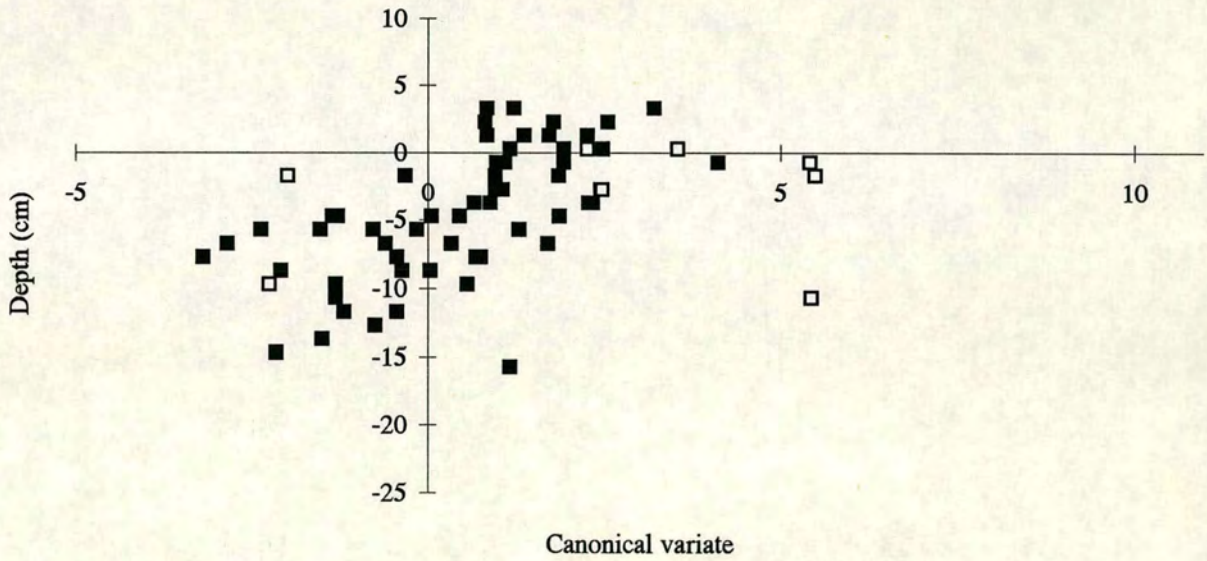


Figure 5.5 e: Distribution of outliers at 717m from Creag Fhiaclach.

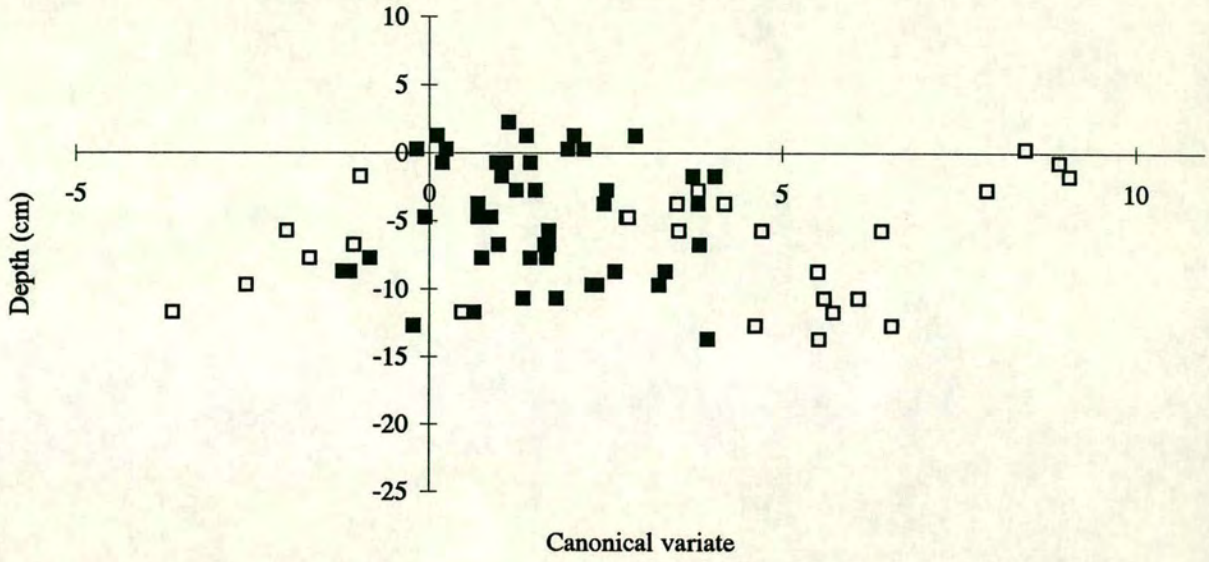


Figure 5.5 f: Distribution of outliers at 758 m from Creag Fhiaclach.

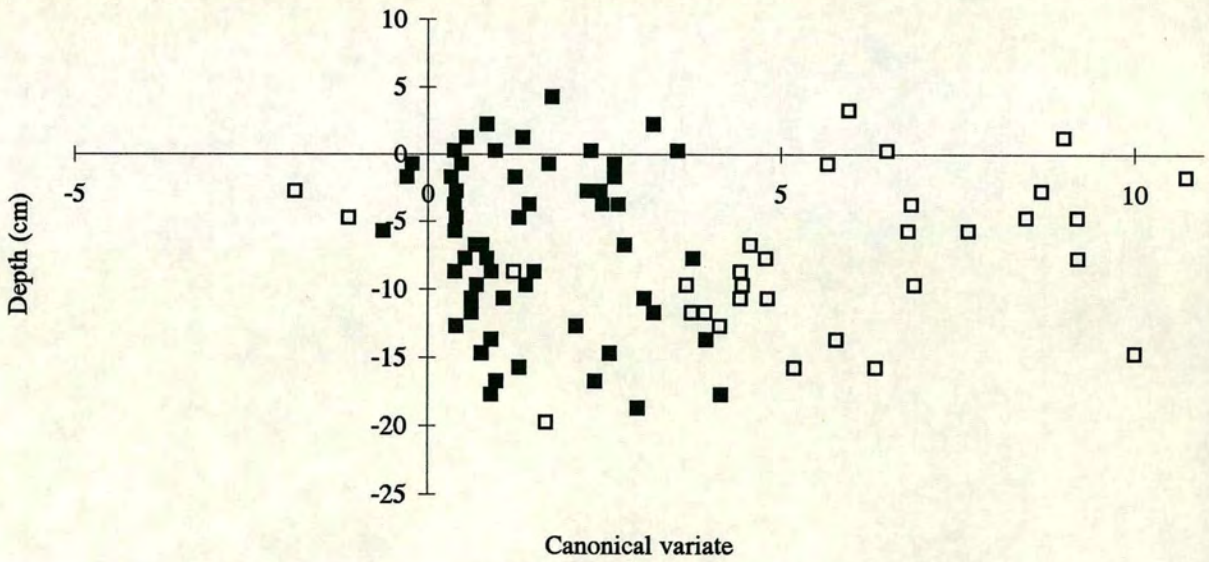


Table 5.6: Ranked results from PCA on transformed covariance matrix. Columns labelled axis one - four contain the codes for palynomorphs, with the corresponding eigenvector loadings in the next column.

Axis one	EVL	Axis two	EVL	Axis three	EVL	Axis four	EVL
Nebe col	0.78	Graminea	0.56	*Assu mus*	0.76	*Call vul*	0.57
Pinu syl	0.57	*Eugl rot*	0.46	*Eugl rot*	0.66	*Pseu men*	0.49
Eugl rot	0.35	*Nebe col*	0.38	*P. nidulus*	0.29	*Epilobium*	0.49
Assu mus	0.33	Cyperace	0.34	Cyperace	0.07	*Juni com*	0.48
Cyperace	0.17	*Assu mus*	0.33	*Pinu syl*	0.04	Eric und	0.45
Pediastrum	0.13	*Betula*	0.18	Eric und	0.04	*Sela sel*	0.41
P. nidulus	-0.07	*Empetrum*	0.03	*Blec spi*	0.03	*Blec spi*	0.41
Potentila	-0.19	*P. nidulus*	0.00	*Juni com*	-0.01	*Myri Cor*	0.41
Erica	-0.24	*Lyco cla*	-0.06	*Potentila*	-0.03	*Diph alp*	0.32
Empetrum	-0.24	*Sphag*	-0.05	*Call vul*	-0.03	*Potentila*	0.39
Vaccinium	-0.24	*Call vul*	-0.04	*Pseu men*	-0.02	*Pediastrm*	0.40
Myri Cor	-0.25	*Erica*	-0.14	*Diph alp*	-0.04	*Alnu glu*	0.28
Graminea	-0.26	*Vaccinium*	-0.30	*Epilobium*	-0.05	*P. nidulus*	0.20
Blec spi	-0.26	*Alnu glu*	-0.26	*Empetrum*	-0.04	*Vaccinium*	0.21
Eric und	-0.27	*Potentila*	-0.36	*Sela sel*	-0.06	*Tilletia*	0.19
Alnu glu	-0.29	*Diph alp*	-0.40	*Pediastrm*	-0.10	*Erica*	0.03
Pseu men	-0.29	*Blec spic*	-0.39	*Alnu glu*	-0.10	*Nebe col*	0.12
Epilobium	-0.29	*Tilletia*	-0.38	*Lyco cla*	-0.09	*Empetrum*	0.12
Juni com	-0.29	*Pediastrm*	-0.37	*Myri Cor*	-0.07	*Lyco cla*	0.15
Sela sela	-0.30	Eric und	-0.50	Graminea	-0.13	*Assu mus*	0.01
Lyco clav	-0.31	*Myri Cor*	-0.54	*Vaccinium*	-0.14	Cyperace	-0.09
Diph alp	-0.32	*Juni com*	-0.56	*Tilletia*	-0.15	*Eugl rot*	-0.16
Tilletia	-0.38	*Sela sel*	-0.57	*Erica*	-0.16	*Sphag*	-0.16
Sphag	-0.40	*Epilobium*	-0.63	*Sphag*	-0.26	*Pinu syl*	-0.31
Betula	-0.56	*Pseu men*	-0.64	*Betula*	-0.28	Graminea	-0.50
Call vul	-0.72	*Pinu syl*	-0.76	*Eugl rot*	-0.46	*Betula*	-0.55

Figure 5.6: A covariance biplot representation of the site and species scores for the pollen assemblages from Creag Fhiaclach. Species vectors are amplified by a factor of 4.5.

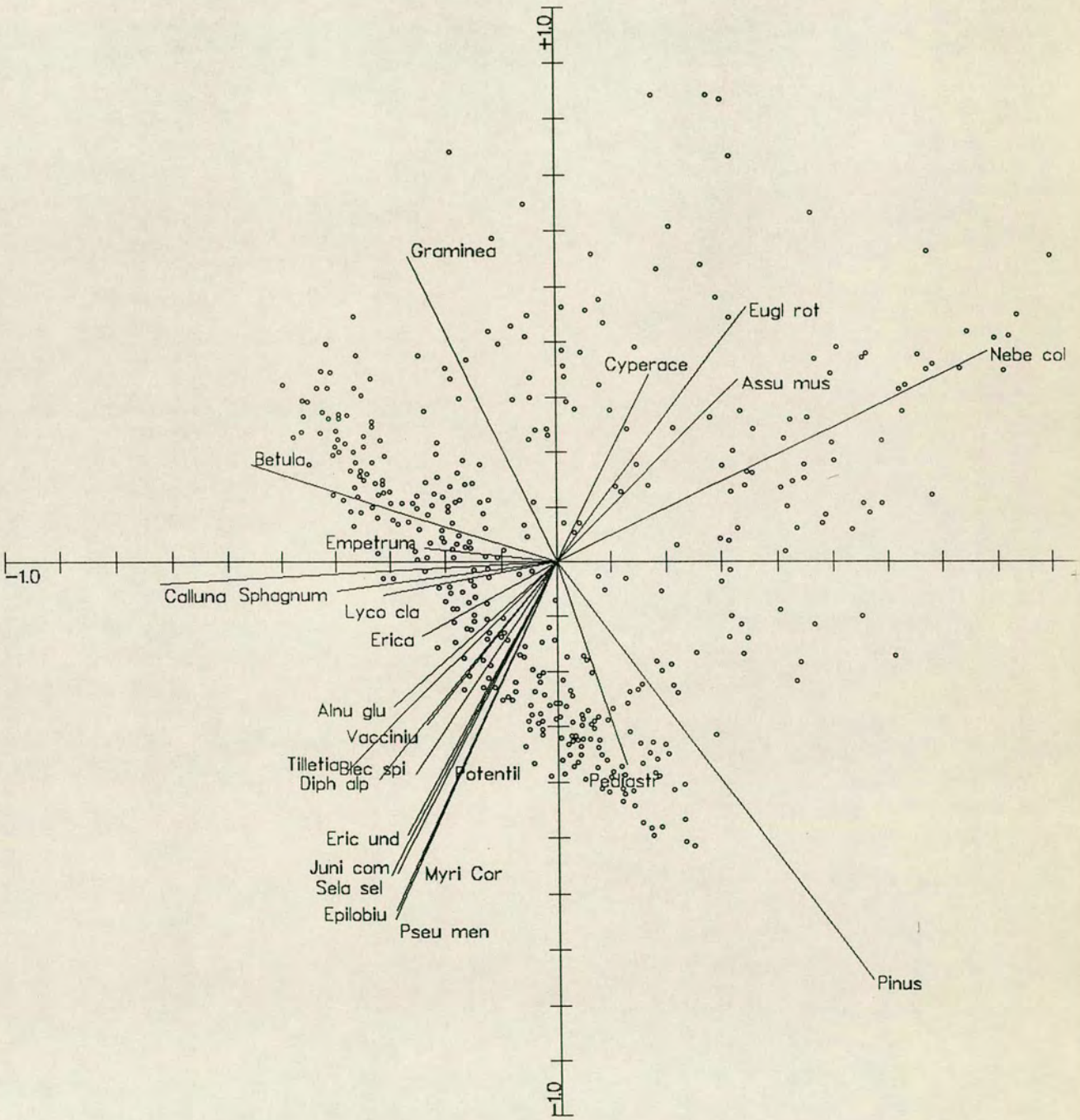


Table 5.7: Summary table of results of PCA of pollen data from Creag Fhiaclach.

Axes	1	2	3	4	Total variance
Eigenvalues					1.00
	0.28	0.20	0.14	0.10	
Cumulative percentage variance of species data	27.50	47.00	61.40	71.20	

5.3.6 Redundancy analysis

As RDA restricted the ordination axes, the RDA axes therefore explain less of the variation in the data than did the corresponding PCA axes (Table 5.8). The number of constrained axes equals the number of environmental variables (three in this case) and therefore the fourth axis in the RDA output had a higher percentage of the variance because it was the first unconstrained axis.

Table 5.8: Summary of RDA results.

Axes	1	2	3	4	Total variance
Eigenvalues	0.13	0.05	0.02	0.20	1.00
Species - environment correlations	0.72	0.50	0.35	0.00	
Cumulative percentage variance of species data	13.20	17.90	19.60	39.90	
Cumulative percentage variance of species - environment correlation	67.70	91.60	100.00		
Sum of unconstrained Eigenvalues					1.00
Sum of constrained Eigenvalues					0.20

The inclusion of product variables of the environmental variables increased the variance explained by the first three axes to 27.3% (Table 5.9). However, the inclusion of products raised the variable inflation factors to 413 and 2293 for the first and third axes. Inflation factors over 20 indicate variables that do not contribute to the regression (Montgomery & Peck, 1982). When product variables were not included, the variable inflation factors were all below 1.01. Thus, all further RDA results are based on analysis without variable products.

Table 5.9: Summary of RDA results when variable products were included.

Axes	1	2	3	4	Total variance
Eigenvalues	0.15	0.08	0.05	0.01	1.00
Species - environmental correlations	0.76	0.62	0.57	0.41	
Cumulative percentage variance of species data	15.20	22.80	27.30	28.60	
Cumulative percentage variance of species - environmental relation	50.80	76.10	91.20	95.50	
Sum of unconstrained Eigenvalues					1.00
Sum of constrained Eigenvalues					0.29

The correlation matrix showed that axis one was highly correlated to both environmental axis one and altitude with the correlation coefficient in both cases being 0.72. The highest correlations of the environmental axes to the environmental variables were:

Axis 1 correlated to altitude	-	0.99
Axis 2 correlated to depth	-	0.85
Axis 3 correlated to replicate number	-	0.85

Thus the first axis was constrained to altitude, the second to depth and third to replicate number. The statistical significance of the first axis was tested using a Monte Carlo permutation test (Chapter 3). The F ratio testing departure from randomness of the data was 72.84 and $p = 0.01$ with 3 degrees of freedom.

The orientation of species scores along the first axis differed slightly from the PCA (Table 5.10). *Pinus* dominated the negative end with an eigenvector loading of -0.65. The nearest species to *Pinus* were *Pediastrum* (-0.31) and *Nebela corralis* (-0.29). The positive end was still characterised by *Calluna* (0.43) and *Betula* (0.42). One of the biggest changes between the first RDA and the first PCA axis was the position of Gramineae. In the PCA Gramineae was quite distant from *Betula* and *Calluna*. However in the RDA Gramineae was positioned next to *Betula* with an eigenvector loading of 0.39. The second RDA axis has *Euglypha rotunda*, *Assulina muscorum*, Gramineae and Cyperaceae at the negative end and a number of rare taxa at the positive end. Gramineae and Cyperaceae featured strongly again on the positive end of the third axis, while *Tilletia*

Table 5.10: Ranked results for the four constrained axes from RDA on transformed covariance matrix. Columns labelled axis one - four contain the codes for palynomorph taxa, with the corresponding eigenvector loadings in the next column.

Axis one	EVL	Axis two	EVL	Axis three	EVL	Axis four	EVL
Call vul	0.43	*Epilobium*	0.29	Graminea	0.20	*Nebe col*	0.87
Betula	0.42	*Juni com*	0.29	*Nebe col*	0.16	*Eugl rot*	0.35
Graminea	0.39	*Pseu men*	0.28	Cyperace	0.13	Cyperace	0.29
Sphag	0.20	*Tilletia*	0.27	*Empetrum*	0.10	*Assu mus*	0.29
Lyco cla	0.17	*Sela sel*	0.26	*Betula*	0.06	Graminea	0.08
Empetrum	0.12	*Eric und*	0.24	*Sphag*	0.00	Circle	-0.10
Erica	0.12	*Alnu glu*	0.24	*Erica*	0.04	*Pinu sly*	-0.07
Alnu glu	0.09	*Myri Cor*	0.23	*Vaccinium*	-0.01	*Pediastrum*	-0.11
Diph alp	0.08	*Vaccinium*	0.19	*Potentilla*	-0.03	*Empetrum*	-0.21
Cyperace	0.08	*Call vul*	0.19	Circle	-0.02	*Erica*	-0.19
Circle	0.08	*Diph alp*	0.19	*Pinu sly*	-0.02	*Lyco cla*	-0.19
Tilletia	0.05	*Erica*	0.17	*Sela sel*	-0.03	*Betula*	-0.21
Vaccinium	0.02	*Blec spi*	0.17	*Juni com*	-0.04	*Sphag*	-0.27
Eugl rot	-0.03	*Betula*	0.17	*Myri Cor*	-0.05	*Alnu glu*	-0.29
Assu mus	-0.05	*Lyco cla*	0.15	*Epilobium*	-0.05	*Vaccinium*	-0.30
Blec spi	-0.06	*Potentilla*	0.14	*Blec spi*	-0.06	*Potentilla*	-0.35
Juni com	-0.08	*Pinu sly*	0.13	*Alnu glu*	-0.08	*Blec spi*	-0.41
Sela sel	-0.08	*Pediastrum*	0.13	*Eugl rot*	-0.07	*Tilletia*	-0.41
Potentilla	-0.10	*Sphag*	0.12	*Pseu men*	-0.08	*Diph alp*	-0.41
Eric und	-0.11	*Empetrum*	-0.06	*Pediastrum*	-0.08	*Eric und*	-0.47
Epilobium	-0.13	*Nebe col*	-0.10	*Diph alp*	-0.10	*Call vul*	-0.47
Myri Cor	-0.14	Cyperace	-0.13	*Call vul*	-0.13	*Juni com*	-0.51
Pseu men	-0.14	Circle	-0.11	*Eric und*	-0.13	*Myri Cor*	-0.48
Nebe col	-0.29	Graminea	-0.21	*Lyco cla*	-0.16	*Sela sel*	-0.52
Pediastrum	-0.31	*Assu mus*	-0.38	*Assu mus*	-0.21	*Epilobium*	-0.55
Pinu sly	-0.65	*Eugl rot*	-0.43	*Tilletia*	-0.23	*Pseu men*	-0.56

characterised the negative end. *Tilletia* is a fungal symbiont of *Sphagnum* and the distributions of the two taxa should be similar. However, *Sphagnum* was close to the origin and thus contributed little information to this axis. Being the first unconstrained axis, variation left unexplained by the environmental variables on the first three will be accounted for on axis four. The negative end of axis four was predominantly of rare taxa and *Calluna*. The positive end was a rhizopod-Cyperaceae community. *Pinus* and Gramineae were both close to zero on axis four.

Sample scores on this first axis varied from -3.5 to about 3. Sample scores along the first axis are plotted against depth for each altitude in Figure 5.7. Pollen spectra from the ten cores taken within the *Pinus* forest had sample scores of -3.5 to 0.5, though most were negative. The reverse was true at 758 m. Here spectra had sample scores of between 3 and -0.5, though most were positive. Pollen spectra from cores at the treeline (648 m) had widely fluctuating loadings on axis one. These fluctuations were not synchronous. Above the treeline at 707 m most pollen spectra are positive. However, replicates four and five below -2.75 and -4.75 respectively have consistently negative values to the base of each core. At 717 m both replicates in these positions revert to being mostly heath pollen assemblages. There are a few spectra from each core that are negative but these are only slightly so. In addition two spectra from replicate two have slightly negative scores. Other than these the remaining spectra at 717 m are all heath assemblages.

5.4 Discussion

5.4.1 Pollen diagrams

A previous pollen diagram from Creag Fhiaclach by Budworth (1984) also showed dominance by *Pinus* and *Calluna*, with other taxa being poorly represented. Taxonomic impoverishment is to some extent a function of the pollen count as larger counts are more likely to incorporate rarer taxa. This can be very important if an indication of all components in the vegetation is required (Faegri & Iversen, 1975). This present study required primarily an accurate estimation of the P*100/(P+C) pollen quotient and therefore a pollen count of 300 was determined sufficient. However, a larger count may have revealed more taxa as shown in the regional pollen spectrum Figure 4.1.

Figure 5.7 a-f: RDA sample scores for pollen assembladges from Creag Fhialach, Cairngorms. The x axis represents the first constrained ordination axis and the y axis is depth. Depth is shown as positive for the litter and unconsolidated peat and is negative for consolidated peat. Symbols represent □ replicate 1, ◊ replicate 2, Δ replicate 3, ◆ replicate 4 and ■ replicate 5.

Figure 5.7 a: RDA sample scores for pollen assembladges at 606 m from Creag Fhiaclach.

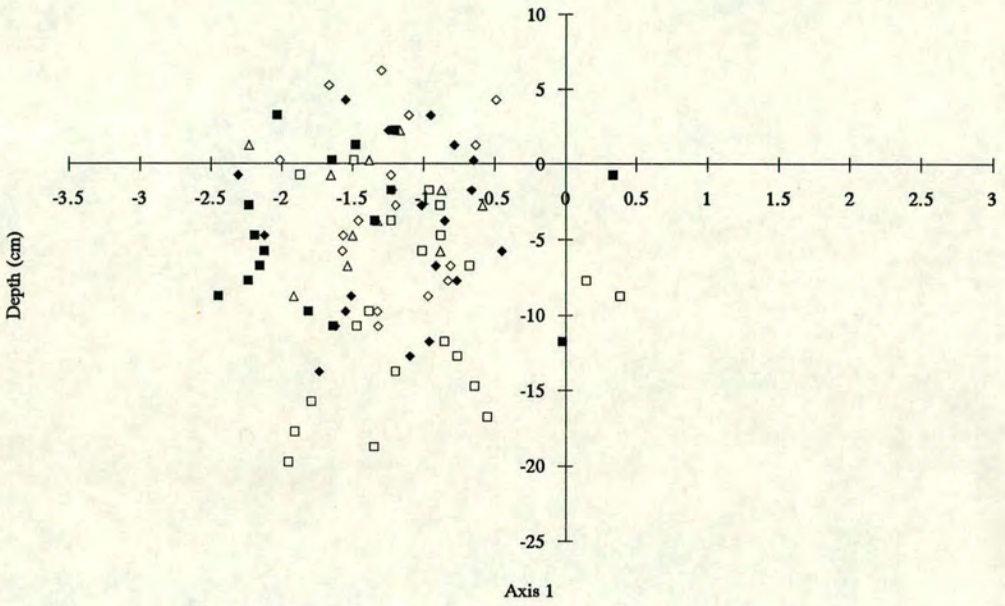


Figure 5.7 b: RDA sample scores for pollen assembladges at 624 m from Creag Fhiaclach.

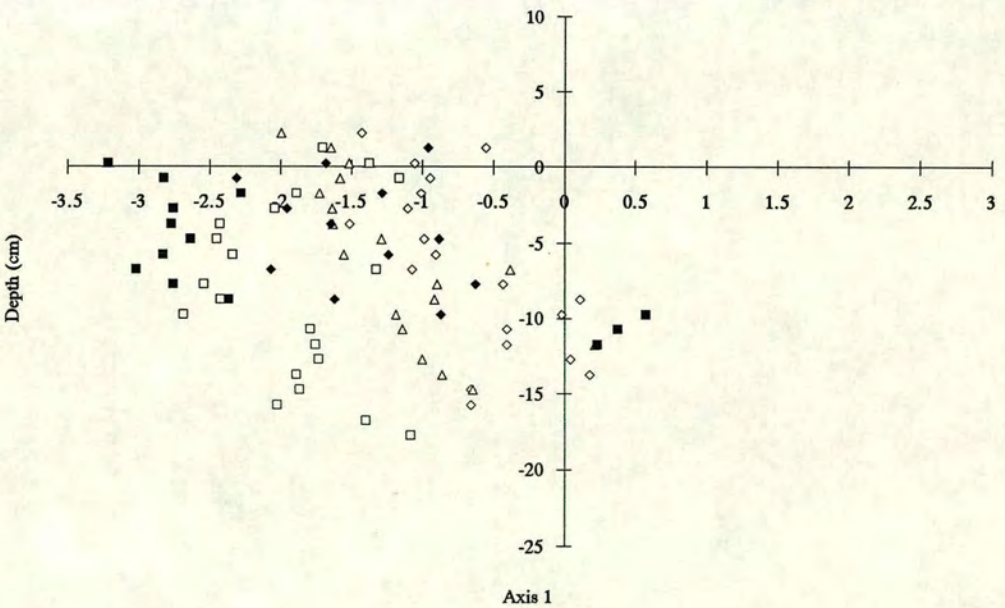


Figure 5.7 c: RDA sample scores for pollen assembladges at the treeline (648 m) from Creag Fhiaclach.

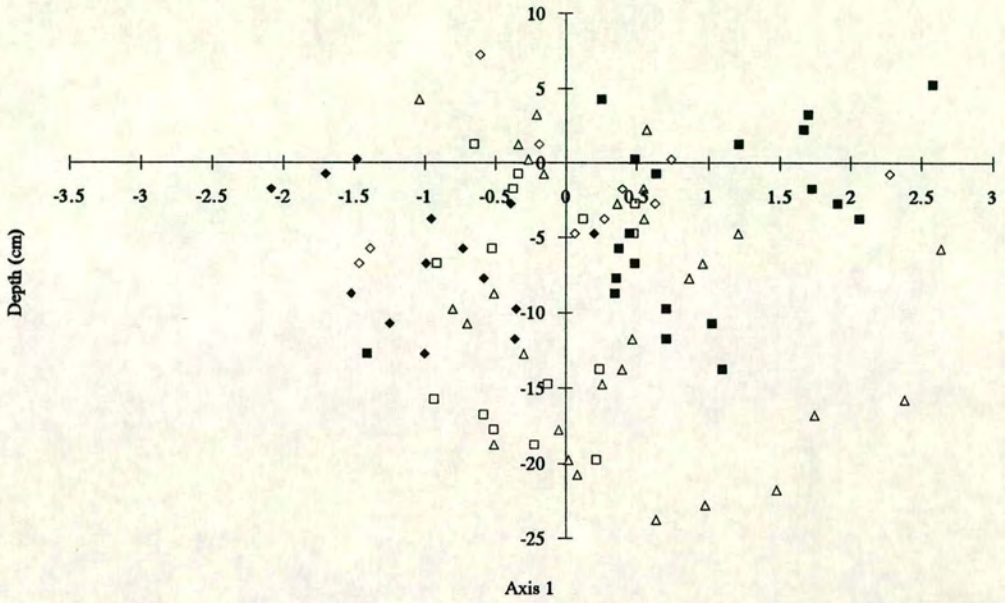


Figure 5.7 d: RDA sample scores for pollen assembladges at 707 m from Creag Fhiaclach.

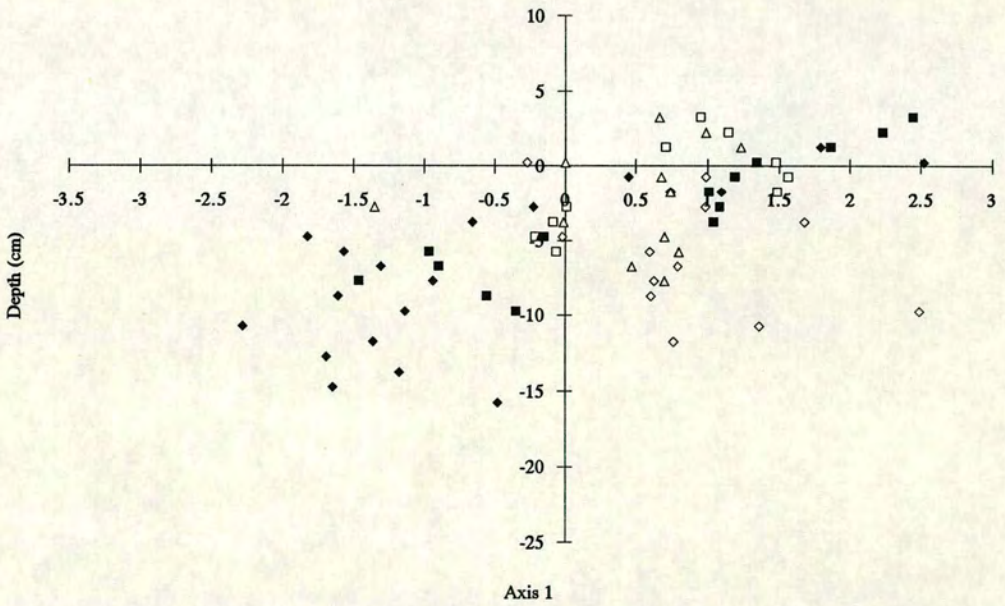


Figure 5.7 e: RDA sample scores for pollen assembladges at 717 m from Creag Fhiaclach.

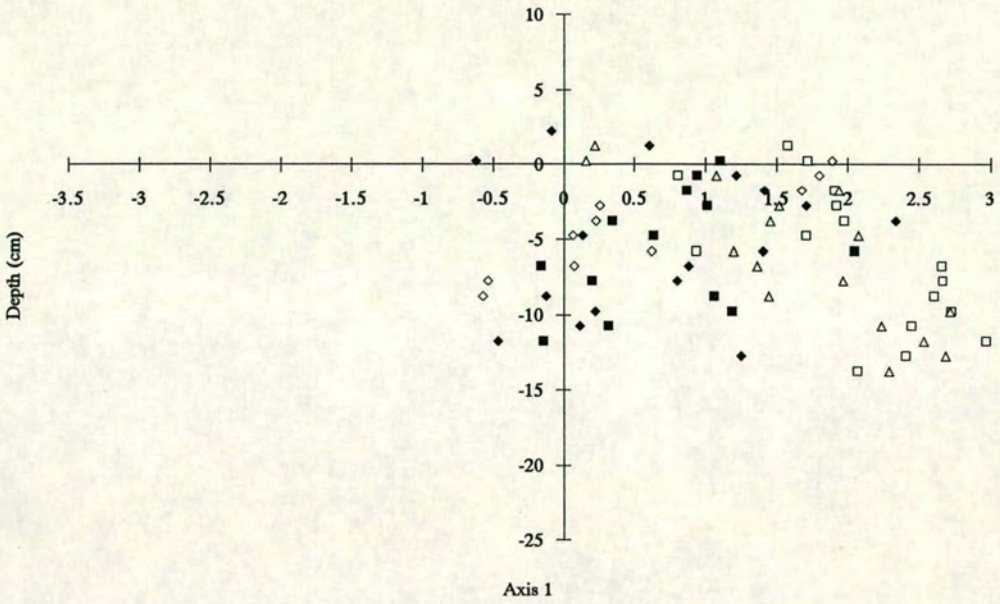
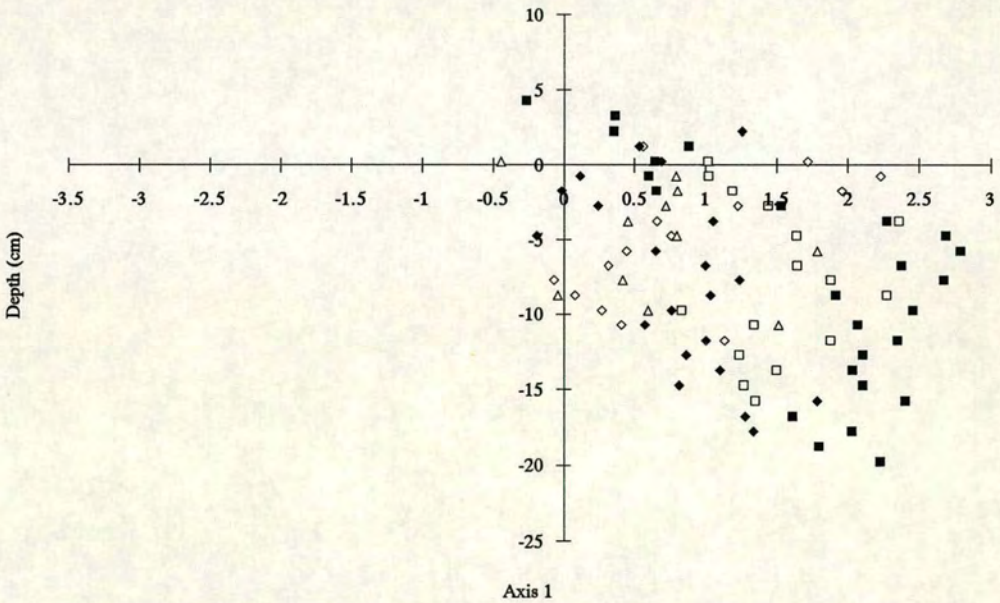


Figure 5.7 f: RDA sample scores for pollen assembladges at 758 m from Creag Fhiaclach.



Pollen diagrams by Pears (1968a) from Carn Mor, Scor Mor and Eidart in the Cairngorms are more taxonomically rich than the diagrams presented here from Creag Fhiaclach. The commonest arboreal taxa in Pears' diagrams were *Pinus*, *Betula*, and *Corylus*, with lesser representation from *Salix, Quercus, Alnus, Ulmus* and *Carpinus*, with the last four being restricted to lower altitudes. The contribution of *Corylus* is particularly notable at around 20%. In the non-arboreal pollen taxa there were good representations of Gramineae, Cyperaceae, Eriaceae, Herbs, *Sphagnum* and Filicales.

The bottom of the profile (170 cm) from Carn Mor (603 m) had a *Betula - Pinus - Corylus* dominated assemblage (Pears, 1968a). This assemblage has been found in other pollen diagrams from Scotland (Birks, 1972, 1975; Pennington, *et al.*, 1972 and O'Sullivan, 1974, 1976) and dated to 7500 BP. The Boreal-Atlantic transition (125 cm) was identified from a decline in the AP to NAP ratio. The upper 50 cm of the profile showed a dramatic increase in the Ericoids associated with accumulating Gramineae and Cyperaceae curves. These curves suggest that predominantly *Pinus* forest was present at Carn Mor from 7500 BP to this decline in the AP curve at 50 cm. The pollen profile from Sgor Mor (716 m) either does not extend back to the Boreal *Betula - Pinus - Corylus* woods or these woods never reached this altitude. Again the top section of the curve from 30 cm has a high representation of Ericoid pollen indicating that the treeline was at lower altitudes to at least this point. However, Pears ascribes an earlier decrease in the AP curve at 75 cm to the decline in the treeline. The Ericoid curve between 75 and 30 cm is a series of three peaks and troughs and could indicate patchy peat initiation. Representation of Ericoids was much reduced throughout the pollen profile from the highest site, Eidart (917 m), and Pears suggests that trees never grew at this altitude.

Turner's (1984) interpretation of treelines at Cross Fell was largely correct in that she assumes that a large local herb pollen indicates vegetation above treeline. However, the top of profiles from Cross Fell South and Cross Fell East showed reducing herb pollen and there has been no other evidence of trees there to day. The tops of these cores are indicating regional pollen and the profiles can be interpreted as a receding treeline with the high herb component being just above the treeline, then the treeline receding to a point where regional aboreal influx becomes significant at higher altitudes.

The three major British palynological horizons identified by Bennett, (1984) i.e., *Corylus* and *Alnus* expansions and the *Ulmus* decline were not seen in the profiles from Creag Fhiaclach. These horizions date to 9000 BP for the *Corylus* expansion (Deacon, 1974), 8000 - 6500 BP for the *Alnus* expansion (Bennett & Birks, 1990) and 5000 BP for the *Ulmus* decline (Smith & Pilcher, 1972). *Pinus* populations in the Scottish Highlands were unaffected by *Alnus* expansion (Bennett, 1984). The absence of *Ulmus* in the pollen assemblages from Creag Fhiaclach suggests that peat initiation on the site was after the elm decline. *Pinus* pollen occurs to the base of the lower altitude cores. *Pinus* has a long history in the region, (Birks, 1975; Bridge *et al.*, 1990; Bennett, 1995, 1996). *Betula* was never more than 20% and was not as prominent as in the Southern Grampians (Durno, 1957).

The pollen profiles from the two lowest altitudes are comparable to zone AF-4 (Birks, 1970), where *Pinus* representation is typically 60% and *Calluna* is the main contributor to the NAP. Birks noted that this zone, is largely restricted to areas where native *Pinus* forest still occurs. This zone has been dated to 7000 years BP in a core from Loch Einich (Birks, 1969). There is no evidence of the *Betula*-dominated AF-3 zone at Creag Fhiaclach suggesting that the cores at Creag Fhiaclach are more recent. A lake core from Loch Garten (O'Sullivan, 1974; 1975) is also very impoverished in relation to the taxa represented, but again *Pinus* pollen is dominant from about 8500 years BP. However, this profile differed from those at Creag Fhiaclach as *Betula* was much more common, usually over 15%. These cores were collected at much lower altitudes and *Betula* may have been a component in the stands.

The change in *Pinus* representation in replicates four and five at 707 m shows no correlation with change in stratigraphic characters. This is in contrast to the pollen profiles of O'Sullivan (1973b) at Abernethy, where changes in the pollen assemblages coincided with the F_2-H boundary. No site at Abernethy had continuous *Pinus* cover, or at least no continually high *Pinus* representation and it is likely that there has been a dynamic relationship between forest and heath even at lower altitudes. O'Sullivan's (1973b) diagrams were also taxonomically poor but showed that *Calluna* dominated heath has persisted in Abernethy since 400 AD.

5.4.2 Interpretation of P*100/(P+C) quotients

The consistently low P*100/(P+C) quotients in the profiles from 758 m indicate that the treeline at Creag Fhiaclach has probably not attained this elevation within the history of these pollen profiles. There is a theoretical possibility that the treeline could have reached this altitude and then receded to a lower altitude within the time span marked by two sampling depths. Two sampling depths may on average be separated by anything from one to five decades on the basis of the radiometric chronologies given in Chapter 7. If such a rapid advance and retreat had occurred it is highly unlikely that this could have remained undetected across all replicates. Equally the low quotients at this altitude indicate that the treeline has never decreased in elevation to the extent where the influence of higher exposure would have decreased the flower production to the extent observed at the modern high-altitude sites.

Profiles from the lowest two altitudes had mostly high P*100/(P+C) quotients. In Chapter 4 it was demonstrated that a high *Pinus* representation could be indicative of either a within-forest or a high altitude heath pollen assemblage. Again theoretically these pollen quotients could be derived from high altitude assemblages. As samples from all depths at 758 m show that the treeline has been consistently below this altitude it is unlikely that the quotients from below the treeline were ever those of high altitude heaths. Some pollen assemblages, from various depths at the two lowest altitudes, had quotients similar to mid-altitude heath with heavily flowering *Calluna* from just above the treeline. The occurrence of these low quotients was erratic. They do not appear to represent fluctuations in the treeline. The structure of native pine woods is such that gaps occur naturally in the canopy. Gaps will influence the light climate on the forest floor allowing *Calluna* to flower more heavily. Dense patches of *Calluna* do occur in present day gaps at Creag Fhiaclach. The net effect of gaps is that pollen spectra have the characteristics of mid-altitude heath spectra. While gaps can be readily detected from modern pollen deposition (Andersen, 1974; Bradshaw, 1981) a gap may need to be present for several decades before it is a detectable signal in a sub-fossil pollen spectrum.

Fluctuations in quotients at the treeline appear to reflect the dynamics of the forest-heath interface. As described in Chapter 2 there are three main contributors to the vegetation at the treeline; *Pinus*, *Calluna* and *Juniperus communis* which form a mosaic with each

species locally dominant within each patch. The approximate composition of vegetation at the treeline in terms of ground cover can be seen in Appendix I.

Patchiness of the current environment in relation to modern pollen influx at the treeline can be seen from the high standard errors associated with the *Calluna* flowering density from this altitude (Figure 4.3). A rapid turnover of this mosaic would result in a stable quotient down the profile through averaging several cycles within each sample. Figure 5.2 shows this is clearly not the case. All cores displayed distinct fluctuations between forest and heath assemblages. The presence of distinct and not simply intermediate quotients between forest and mid-altitude heath types indicates that the changes over time from one community to another must take decades or more. This is certainly true of the mature krummholtz at the treeline which range in age from 100-250 yrs (Grace & Norton, 1990).

In samples initially entered into the discriminant analysis the treeline class was virtually indistinguishable from the forest class. This was hardly surprising for three reasons. Firstly, the treeline is in the region of the direct influence of the *Pinus* stand. Despite the heavy *Calluna* flowering there is a significant *Pinus* influx to the pollen spectrum from the adjacent stand. Secondly, forest components of the mosaic may be longer lived than the *Calluna* or *Juniperus communis* components. This will have the effect of a long input of *Pinus* pollen, which will dampen the amplitude of the shorter *Calluna* signal. Finally, *Juniperus communis* stands may also result in a high P*100/(P+C) quotient similar to forest cover. This is because the dense *Juniperus communis* canopy prevents the deposition of local *Calluna* pollen, producing a pollen influx high in the more widely distributed *Pinus* pollen. Distribution in *Juniperus communis* as a component of present day vegetation with altitude is shown in Appendix I. *Juniperus communis* leaves a poor pollen record as it does not flower frequently or heavily at this altitude, and it is dioecious so at least some cover will be by plants that will not produce any pollen. In addition *Juniperus communis* pollen is not well preserved in the pollen record, tending to disintegrate along the axis (Bertsch, 1961) so the extent of this phenomenon is difficult to determine from the pollen assemblages. Effectively then, *Juniperus communis* cover will result in a pollen spectrum with a quotient indistinguishable from that of *Pinus* cover. This hypothesis is outlined more fully and tested in Chapter 6.

There are three possible interpretations of the high quotients below -3.75 cm in replicate four and five at 707 m:

1. They may indeed represent a higher elevation treeline in the past. These two replicates come from the southern-most end of the ridge and the reduced exposure may have been sufficient to enable tree establishment above the current treeline.
2. These high quotients could have been caused by a drop in the altitude of the treeline to give high altitude heath ratios in these replicates.
3. Low pollen producing local dominants in the vegetation, e.g., *Juniperus communis*, may have restricted the influx of local *Calluna* pollen as outlined above.

If the treeline did decrease in elevation to deposit such a spectrum at 707 m, then high-altitude spectra would be expected at 717 m at a comparable point in time. Figure 5.2 d shows that all samples from replicate five are definitely consistent with mid-altitude heath down the entire core. Replicate four is not as clear cut, with a few quotients lying between 30% and 40%.

Other than a few samples from replicate four, only replicate two has consistent high quotients at 717 m (Figure 5.2 e). Again, there are three alternative interpretations: treeline rise, treeline fall and suppression of local pollen deposition by a low pollen producing dominant. A treeline fall can be discarded as a fall would also produce similarly high quotients at 758 m which are absent. Similarly in considering a treeline rise as a cause of high quotients in replicate two at 717 m, there are no supporting high quotients at 707 m. Treelines can advance as small isolated groups of trees (Stevens & Fox, 1991). These quotients could therefore represent the initial stages of treeline advance. Low pollen producing dominance is considered more fully in Chapter 6.

Simple quotients, have the advantage of being readily calculated and are sufficient for the interpretation of most of the pollen data. However, quotients are ambiguous in distinguishing between forest and high altitude heath spectra. Other qualitative differences may also occur in forest gaps and where low pollen producing dominants such as *Juniperus communis* and *Juncus trifidus* occur. There is much more information in the pollen data than a simple P*100/(P+C) quotient. To fully interpret the palaeoecological data, analysis of the full taxonomic data is desirable.

5.4.3 Discussion of discriminant analysis

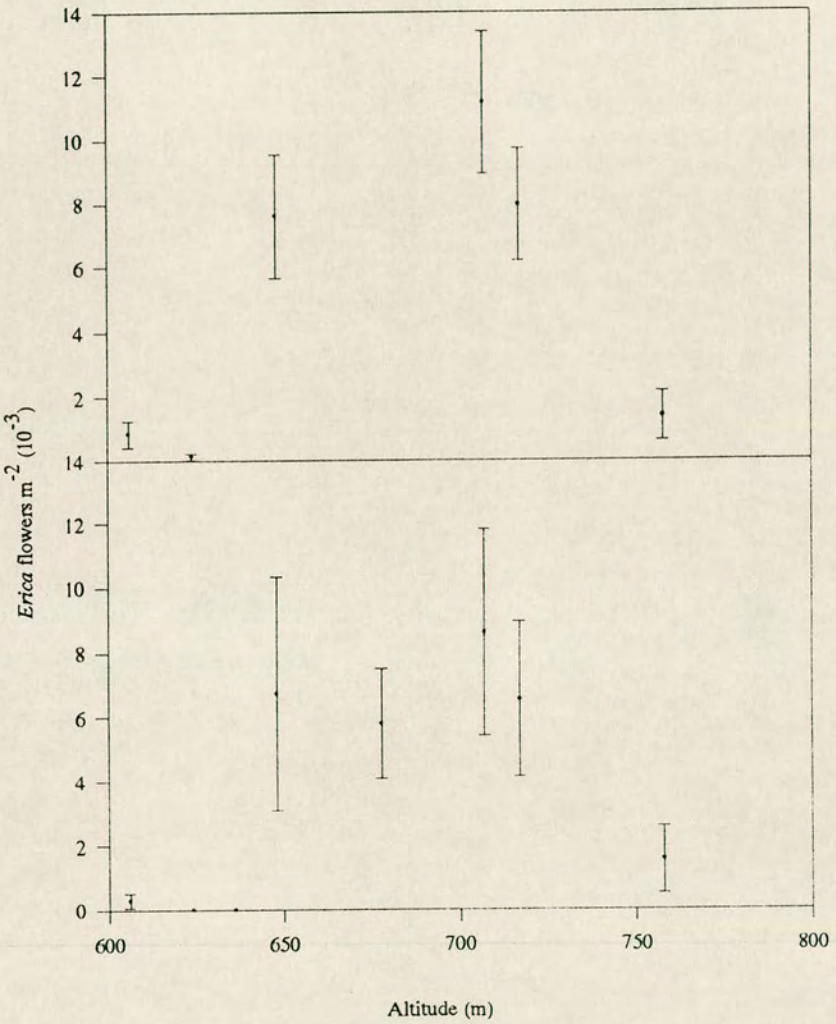
It required more than the information contained in the distribution of *Pinus* and *Calluna* to correctly classify all the surface samples using discriminant function analysis. The distribution of *Betula*, *Diphasiastrum alpinum*, circular rhizopod morph and *Erica* were required to give a classification in which no samples were misclassified.

Betula pollen was the second most common arboreal pollen type in the pollen spectrum from Ciste Mhearad (Figure 4.1) and can be considered as a regional pollen type. The high influx of *Betula* pollen in heath spectra, where regional pollen influx is less confounded by the local pollen signals of the *Pinus* forest stand or swamping from *Calluna* at the treeline is not unexpected. Unlike *Betula*, *Diphasiastrum alpinum* was not encountered in the regional pollen signal as recorded from Ciste Mhearad. *Diphasiastrum alpinum* is a species of upland heaths between 450 and 1220 m (Page, 1982) and because of its creeping growth habit most of its spores will be locally deposited. The circular rhizopod morph(s) were also associated with the heath pollen spectra, though insufficient is known about their ecology to draw any conclusions from this. As opposed to *Betula*, *Diphasiastrum alpinum* and the circular rhizopod morph which were associated with heath spectra, *Erica* was associated with lower altitude forest-covered spectra. While it is theoretically possible to distinguish between *Erica tetralix* and *Erica cinerea* pollen types (Moore *et al.*, 1991), this is in practice a very difficult distinction to make. Thus the *Erica* pollen from Creag Fhiaclach may be a combination of both species. However, only *Erica cinerea* occurs in the present day vegetation. Both *Erica* species are insect pollinated and will be under-represented in the pollen record. The distribution of *Erica cinerea* flowers was measured at Creag Fhiaclach in 1992 and 1993 and is displayed in Figure 5.8. The altitudinal distribution of *Erica* flowers was exactly opposite to the percentage distribution of *Erica* pollen. This may be a Type I error because of the very small amounts of *Erica* pollen encountered caused by too small a pollen sum.

5.4.4 Discriminant analysis results compared with quotients

There is a general concordance between the results from the discriminant analysis and the distribution of P*100/(P+C) pollen quotients. The pattern of predominantly heath type spectra at higher altitudes, predominantly forest at 606 and 624 m, fluctuations at the treeline, and a possible indication of tree cover at 707 m were found in both analyses.

Figure 5.8: Variation in *Erica* flowering with altitude in 1992 and 1993 from the six lowest altitudes spanning the treeline. Comparison of 15 means in 1992 and 5 means in 1993, standard errors are shown as error bars.



Spectra from replicates two and three at 758 m that were classified as forest on the basis of their discriminant functions had P*100/(P+C) quotients of less than 20%. In the final discriminant function, *Erica* has a large influence on the regression of spectra from -5.75 cm in replicate two and -0.75, -1.75, -2.75 and -4.75 in replicate three (Table 5.11a). These samples are being classified as forest on the basis of their *Erica* content.

The worked example of the discriminant function for the apparently aberrant forest samples is given in Table 5.11a. This clearly demonstrates the influence of *Erica* representation on the classification of these pollen assemblages. The format of Table 5.11b is as for Table 5.11a, with the exception that it is the heath discriminant function that is being calculated this time.

Table 5.11a: A worked example of the calculation of the discriminant function for samples classed as forest by the discriminant analysis with quotients typical of heath pollen assemblages from replicate three at 758 m. The first column is depth. The intercept is given in column two and functions of the five contributing taxa are calculated according to the discriminant function (Table 5.3). The column headed F gives the final calculation with the forest regression. The calculation of the regression for heath is given in the column headed H for comparison. The discriminant score is calculated using both forest and heath discriminant functions and the case is assigned to the class with the largest value. In the final column the P*100/(P+C) pollen quotient is given for comparison.

Depth	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	Circle	F	H	Quotient
-5.75	-7.5	3.49	-0.20	4.68	0	0	0.47	-1.75	12.71
-0.75	-7.5	3.78	-0.40	4.68	0	0	0.56	-0.26	17.78
-1.75	-7.5	4.07	-0.40	4.68	0	0	0.86	-0.22	18.32
-2.75	-7.5	4.66	-0.40	9.37	0	0	6.13	-0.44	21.13
-4.75	-7.5	3.49	-0.60	9.37	0	0	4.75	0.83	14.59

Table 5.11b: Calculation of heath function.

Depth	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	Circle	H	F	Quotient
-5.75	-3.4	0.52	1.45	-0.31	0	0	-1.75	0.47	12.71
-0.75	-3.4	0.56	2.89	-0.31	0	0	-0.26	0.56	17.78
-1.75	-3.4	0.60	2.89	-0.31	0	0	-0.22	0.86	18.32
-2.75	-3.4	0.69	2.89	-0.62	0	0	-0.44	6.13	21.13
-4.75	-3.4	0.52	4.34	-0.62	0	0	0.83	4.75	14.59

Both the quotients and the discriminant classes fluctuated with depth in replicate four at 717 m. Some spectra with quotients under 30% were classed as forest by the discriminant function and *vice versa*. Calculation of these functions are given in Tables 1-2 in Appendix V. Spectra from 2.25 cm and -10.75 cm (Table 2, Appendix V) are the spectra where the discriminant classification and the quotients disagree. The second two spectra were included for comparison and here the discriminant classification and the quotients concur. There are two things of note. Firstly, the disparity between the quotients and the discriminant classification appears to be based here on the distribution of the circular rhizopod morph(s). When these morph(s) were removed from the pollen data both spectra were classed as forest samples, with canonical variables of 1.85 and 0.94 respectively. Secondly, the first sample was also the surface sample originally used to determine the discriminant function. This sample was misclassified when the default F-to-enter values were used. Similarly to the example in Table 1 (Appendix V), at -5.75 cm in replicate one the occurrence of *Erica* pollen drove the discriminant function to classify the pollen spectra as a forest type even though the quotient was 21.9%. Two spectra from replicate two were classified as forest, but these both had quotients over 40%. However, seven spectra were classed as heath with high quotients. Table 3 (Appendix V) indicates that it is the presence of *Betula* pollen which is influencing this classification.

There are numerous cases of this type of disparity in classification between the discriminant method and quotients at 707 m. In replicates one, two and three all spectra were classed as forest on the basis of their quotients, except the sample from -2.75 in replicate three that had a quotient of 35%. Replicates one, two and three all have at least one sample which was classed as forest by the discriminant analysis. Replicates four and five were nearly all classified as forest below -4.75 cm by the discriminant analysis which was in concordance with the quotients. Replicate four had three exceptions to this. These

three samples from replicate four which were classified as heath by the discriminant analysis appear to have been classified on the basis of *Betula* pollen. *Betula* pollen is the only taxon apart from *Pinus* that affects the discriminant function (Table 4, Appendix V).

At the treeline there were fluctuations in both classifications down all cores. There were four cases where pollen assemblages with quotients over 30% were classed as heath. These four assemblages all had a good representation of *Betula*. Thirteen pollen assemblages with low quotients were classed as forest by the discriminant analysis (Table 5, Appendix V). None of these samples had any representation from *Diphasiastrum alpinum* or the circular rhizopod morph(s). In some cases it is easy to see that it is the presence of *Betula* or *Erica* that is directing the classification, however, in other cases there appears to be only *Pinus* influencing the classification. As the F-to-enter for *Calluna* was reduced to an insignificant level when *Pinus* was entered into the discriminant function *Calluna* could not influence the discriminant classification. *Calluna* did, however influence the quotients and the divergence of the two classifications would be effected by this. In addition, sterile *Juniperus communis* canopies may be affecting the deposition of *Calluna*. This is dealt with in Chapter 6.

Heath pollen spectra occurred in all cores, except replicate two at 606 m. Distribution of heath spectra was erratic. Four of the eight samples classed as heath at 606 m and three of the fourteen samples similarly classed at 624 m had pollen quotients lower than 30%. The remaining samples at both altitudes had quotients ranging from 31-58%. Classification as heath samples was caused by higher than expected representation of *Betula* (Table 6-7, Appendix V). These samples may have occurred in gaps where regional pollen had been deposited or may be the result of local pollen influx from individual trees of *Betula* within the forest.

5.4.5 Interpretation of the principal component and redundancy analyses

The amount of variation explained by the PCA and RDA axes was very low. Pollen data are usually noisy (Birks & Gordon, 1985) and this data set contained many zero values. The very low sum of constrained eigenvalues (0.196) in the RDA shows clearly that the known environmental variables explain very little of the observed variation. Of the variation that was accounted for, altitude was the main factor. The correlation between

species axis one and environmental axis one (altitude) demonstrates that the first RDA axis was a *Pinus-Calluna* gradient. The negative end of the axis was composed of forest pollen assemblages and the positive end of heath assemblages. *Betula* and Gramineae were well represented in the regional pollen spectrum (Figure 4.1) and their close association with *Calluna* at the positive end of the first RDA axis is unsurprising. Gramineae, however were only weakly associated with the heath pollen assemblage on the first PCA axis. Gramineae also played no part in the discriminant function analysis. On the species-site biplot (Figure 5.6) Gramineae were very strongly negatively correlated to *Pinus* and if Gramineae had occurred in sufficient numbers to be reliable then a *Pinus*-Gramineae quotient may have been a useful determinant of apparent altitude.

Two interpretations of the second PCA axis are possible. The second axis may be separating low altitude *Pinus* dominated assemblages from Cyperaceae, Gramineae, and rhizopod-rich flushes. Alternatively, on the basis of the RDA the second axis could be interpreted in terms of differential preservation. Many of the taxa with high loadings at the positive end of axis two were rare in the data set. If the pollen of these taxa decompose at even a slightly faster rate than the more abundant taxa their contribution to the pollen sum will soon decline. *Euglypha rotunda* and *Assulina muscorum* characterised the negative end of the second axes. Although rhizopods have very tough tests their survival in soils is much lower than would be expected, with an 89-98% loss in the first two weeks (Lousier & Parkinson, 1981). However, the preservation state of the pollen taxa in the peat deposits was excellent and would not lend support to this hypothesis. Further ecological interpretation of rhizopod data is impeded by a lack of adequate knowledge on species - environment relationships. The main factors affecting spatial distribution and species composition are moisture, pH, nutrients/detritus availability, oxygen and light. Reviews of the influences of these factors are given by Tolonen (1986) and Ogden & Hedley (1980). Other ecological processes, such as inter- and intra-specific competition appear to have received little attention and an experimental approach to determining the ecology of rhizopods using controlled culturing techniques was found to be of limited success (Heal, 1964).

The third RDA axis was constrained to replicate number and hence because of the geometric nature of the sampling grid the negative end was weighted to the more northerly

exposed sites and the positive end to southerly sheltered cores. The third axis accounted for 4.5% of the variation in the data set and as such is of very limited assistance to interpretation. However, two general observations can be made. Firstly, the loading of *Tilletia* at the negative end of the axis was because of the high content of *Sphagnum* peat in a core from the northern end of the grid. *Tilletia* is a fungal symbiont of *Sphagnum*. Interestingly, *Sphagnum* has no information content on the third axis. At these altitudes spore production in *Sphagnum* may be sporadic. *Tilletia* spores may therefore be a better indicator of the previous distribution of *Sphagnum* than *Sphagnum* spores. The second point of note is the relative loadings of *Calluna* and *Pinus* on the third axis. *Pinus* had an eigenvector loading of nearly zero while *Calluna* had a more negative (northerly) loading. Interpretation here is highly speculative because of the low amount of information contained on this axis. However, it could be postulated that the position of *Pinus* indicates the uniform longitudinal and hence regional nature of *Pinus* pollen distribution. *Calluna* representation, having more locally deposited pollen, will be more tightly coupled to the distribution of *Calluna* on the site.

6

Effects of sterile *Juniperus communis* canopies on pollen quotients

6.1 Introduction

Davis (1963) was the first to consider the possibility of two different types of vegetation producing the same pollen spectrum. In upland vegetation in Britain, Birks (1973a) questioned what impact unproductive canopies, such as *Racomitrium lanuginosum*, *Luzula spicata* and *Juncus trifidus*, would have on modern pollen spectra. Chapter 5 raised two hypotheses on the possible impact of sterile *Juniperus communis* (refered to henceforth as *Juniperus*) stands on pollen spectra. Firstly, dense *Juniperus* canopies may reduce the deposition of local *Calluna* pollen, resulting in a pollen influx proportionately higher in the more regionally distributed *Pinus* pollen. Thus *Juniperus* canopies in *Calluna* heath above the treeline may result in forest-type pollen assemblages. Secondly, a dense *Juniperus* canopy will also reduce dispersal of pollen from species flowering beneath the canopy, resulting in a high count of other pollen taxa.

These hypotheses could be investigated by examining the distribution of *Juniperus* pollen compared to sub-fossil taxa in the sub-fossil pollen spectra. However, *Juniperus* pollen was insufficiently common in the pollen spectra for this to be reliable. The low representation of *Juniperus* pollen in peats is probably a combination of low production and poor preservation. *Juniperus* pollen is poorly preserved with grains commonly being crumpled (Moore *et al.*, 1991) or split along the axis (Bertsch, 1961). No whole *Juniperus* pollen grains were found in either the modern pollen rain studies or the palynological investigation at Creag Fhiaclach.

Iversen (1954) suggested that the representation of *Juniperus* in pollen diagrams was a function both of the ecology of *Juniperus* and prevailing climate. In describing the Late Weichschelian *Juniperus* peak Iversen hypothesised that *Juniperus* was probably present in abundance, but its growth form was restricted to the prostrate and non-flowering form because of poor climatic conditions. As soon as the climate improved, this pre-existing source proliferated and flowered profusely, producing the Late Weichschelian *Juniperus*

peak. Modern pollen spectra from four *Juniperus* stands in northern Britain support this hypothesis (Birks, 1973a). Birks (1970) found considerable reductions in numbers of *Juniperus* pollen after expansion of, and presumably suppression by, *Corylus* in Abernethy during transition from AF-2 to AF-3. However, even with radiocarbon dating it has been difficult to determine if the early Holocene *Juniperus* peak in Britain was synchronous and if it was related to climate change (Tipping, 1987). In Ireland (Pilcher, 1970) suggested that the *Juniperus* expansion was mediated by soil development rather than directly related to climate.

Representation of *Juniperus* can also be inferred from flowering studies. Birks (1973b) described considerable variation in flowering in *Juniperus*. Birks (1973a), describing the pollen representation of *Juniperus communis* ssp. *nana* in chionophobous communities in Skye, noted that bushes of *Juniperus communis* ssp. *nana* rarely flowered at 305 - 610 m.

In the survey reported here, data were collected in order to test the hypothesis that low pollen producing *Juniperus* canopies reduce the contribution of *Calluna* to the modern pollen rain under the canopies thereby producing pollen spectra above the treeline which are typical of *Pinus* forest.

6.2 Method

Moss polsters were collected from transects through eight *Juniperus* patches at Creag Fhiaclach in April 1994. The use of moss polsters to determine modern pollen rain has been discussed in Chapter 4. A *Juniperus* 'patch' was defined as having at least 70% *Juniperus* cover. The patches were of various dimensions and of varying distances from the treeline (Table 6.1). *Juniperus* is shade intolerant (Miles & Kinnaird, 1979) and extensive patches were infrequent under the *Pinus* canopy. Only two patches were therefore taken from below the treeline.

Subsequently, a transect was laid out through each patch perpendicular to the treeline. The vegetation in 10 cm x 10 cm quadrats was then recorded from beneath the *Juniperus* canopy. Quadrats were placed so that the first quadrat was in the centre of the patch. Additional quadrats were recorded at 1 m intervals with the last quadrat in each direction being in the *Calluna*-dominated vegetation outside the patch.

Table 6.1: The number of quadrats in eight *Juniperus* patches in Forest (F), Treeline (TL) and Heath (H) habitats and the corresponding number of *Calluna* quadrats. Distances from the treeline are distances on the ground and not altitudinal differences.

Patch number	Distance from treeline	Diameter (m)	F	TL	H
1	45 m below	6.2	6		
2	30 m below	8.8	8		
3	15 m above	4.7			4
4	treeline	3.1		3	
5	treeline	2.2		2	
6	5 m above	5.0			5
7	15 m above	2.8			3
8	treeline	9.3		9	
	Number of quadrats within	*Juniperus*	14	14	12
	Number of quadrats in surrounding	*Calluna*	4	6	6

The sampling design was constrained by the layout of the vegetation on the ground and has an inherent bias as there were 40 quadrats from *Juniperus* canopies and only 16 from *Calluna* canopies. In addition, 35% of the *Juniperus* quadrats were in the two forest patches sampled as opposed to 25% for *Calluna*.

A moss polster was collected from the centre of each quadrat for analysis of the modern pollen rain. The dry weight and percentage species composition of moss polsters were noted. Polsters were prepared for pollen counting by the standard method outlined in Chapter 3; the mean pollen count was 399.

6.3 Results

Composition of vegetation under the *Juniperus* canopy and from the quadrats immediately outside the *Juniperus* canopy are given in Tables 6.2 and 6.3 respectively. Percentage cover of all Ericoids, *Deschampsia flexuosa* and *Trichophorum cespitosum* was much reduced under the *Juniperus* canopy compared with the *Calluna* canopy. Other than a reduction in cover by *Hylocomium splendens* under the *Juniperus* the bryophyte communities under both canopies were very similar.

The pollen in the moss polsters was in a good state of preservation. Pollen profiles across each patch are shown in Figures 6.1 a-h.

Table 6.2: The composition (mean % cover, x and standard error,se) of the vegetation in the quadrats beneath *Juniperus* canopies at Creag Fhiaclach. Means based on a single value are indicated by a *.

Species	Patch 1 (n=6)		Patch 2 (n=8)		Patch 3 (n=4)		Patch 4 (n=3)		Patch 5 (n=2)		Patch 6 (n=5)		Patch 7 (n=3)		Patch 8 (n=9)	
	x	se	x	se	x	se	x	se	x	se	x	se	x	se	x	se
Calluna vulgaris			0.3	0.0	0.3	*	1.7	*	6.0	1.0					2.2	*
Empetrum nigrum			0.1	*	0.3	*	0.3	*			0.2	*				
Erica cinerea									0.5	*						
Juniperus communis	100.0	0.0	78.1	9.5	93.8	4.7	48.3	6.1	77.5	2.5	62.0	6.8	63.3	14.5	72.8	8.2
Pinus sylvestris															0.1	*
Vaccinium myrtillus			0.9	0.0	1.0	0.0					0.6	0.0	6.3	2.7	1.8	1.2
Vaccinium vitis-idaea	1.3	0.2	10.4	1.8	3.8	1.8					1.0	0.0	10.3	5.5	10.3	2.5
Deschampsia flexuosa											1.0	0.0			1.9	0.6
Trichophorum cespitosum			1.6	0.5	0.3	*							1.0	0.0		
Lycopodium clavatum			0.1	*											0.2	*
Blechnum spicant	1.0	1.2	1.0	0.7												
Dicranum scoparium	1.2	0.9													33.9	7.1
Dicranum fuscescens					51.3	10.5			45.0	20.0						
Hylocomium splendens	1.2	0.2	30.6	6.7			40.0	23.6			30.0	11.7	21.7	4.4		
Hypnum cupressiforme	0.2	*	0.3	*									0.3	8	0.2	*
Pleurozium schreberi			0.4	0.0											0.1	*
Polytrichum juniperinum			0.3	0.0			1.0	0.0			4.0	1.3				
Pseudoscleropodium purum			0.1	*							0.4	0.0				
Racomitrium lanuginosum																
Rhytidiadelphus squarrosus					0.5	*					0.2	*			0.1	*
Plagiothecium undulatum	0.2	*	0.1	0.3												
Ptilium crista-castrensis	0.8	*	0.5	0.2	1.3	*	0.3	*								

Table 6.3: The composition (mean % cover, x and standard deviation, se) of the vegetation in the quadrats immediately outside the *Juniperus* patches (n=2) at Creag Fhiaclach. Means based on a single value are indicated by a *.

Species	Patch 1		Patch 2		Patch 3		Patch 4		Patch 5		Patch 6		Patch 7		Patch 8	
	x	se	x	se	x	se	x	se	x	se	x	se	x	se	X	SE
Calluna vulgaris	77.5	2.5	75.0	10.0	80.0	10.0	90.0	10.0	92.5	2.5	82.5	17.5	87.5	12.5	92.5	2.5
Emptrum nigrum	5.0	*			2.5	*					12.5	*				
Erica cinerea													5.0	*	5.0	*
Juniperus communis			2.5	*	0.5	*			0.5	*					0.5	*
Pinus sylvestris																
Vaccinium myrtillus	15.0	5.0	12.5	7.5	3.0	2.0	3.0	2.0	7.5	2.5	7.5	2.5	20.0	10.0	1.0	1.0
Vaccinium vitis-idaea	8.0	7.0	12.5	0.5	20.0	5.0	10.0	0.5	17.5	7.5	10.0	5.0	5.0	0.0	7.5	2.5
Deschampsia flexuosa	5.0	*	10.0	2.5			1.0	0.0			3.0	2.0			5.0	0.0
Trichophorum cespitosum	0.5	*	2.5	5.0	3.5	1.5	1.0	*	3.5	1.5	0.5	*	3.0	2.0		
Lycopodium clavatum																
Blechnum spicant																
Dicranum scoparium	0.5	*													5.0	0.0
Dicranum fuscescens					20.0	5.0			7.5	2.5					2.5	*
Hylocomium splendens	15.0	5.0	10.0	5.0			5.5	4.5	0.1	*	8.5	6.5	3.0	2.0		
Hypnum cupressiforme	0.5	*													0.5	*
Pleurozium schreberi	0.5	*			0.5	*			0.5						0.5	*
Polytrichum juniperinum							0.5	*			0.5	*			0.5	*
Pseudoscleropodium purum			2.5	*							0.5	*			0.5	*
Racomitrium lanuginosum			1.1	1.0	0.5	*	0.5	*								
Rhytidiadelphus squarrosus	3.0	2.0			3.0	2.0			1.5	0.5						
Plagiothecium undulatum							0.5	*			0.5	*	5.5	4.5		
Ptilium crista-castrensis													0.5	*		

Changes in the *Pinus/Calluna* pollen quotient in relation to percentage of *Calluna* cover in the canopy are shown in Figure 6.2 a-h. The Pearson product-moment correlation coefficients are also shown. There was a dramatic increase in the P*100/(P+C) quotient under *Juniperus* compared with under *Calluna*. This effect was apparent even over short distances into the vegetation and in the smallest patch, patch 5, which was only 3 m across. Correlation coefficients were high for all patches, except patch 3 which had a coefficient of -0.56. The remainder of the patches had coefficients ranging from -0.79 to - 0.94. Absolute pollen concentrations of selected taxa as grains per gram of oven-dry moss taxa are shown in Table 6.4.

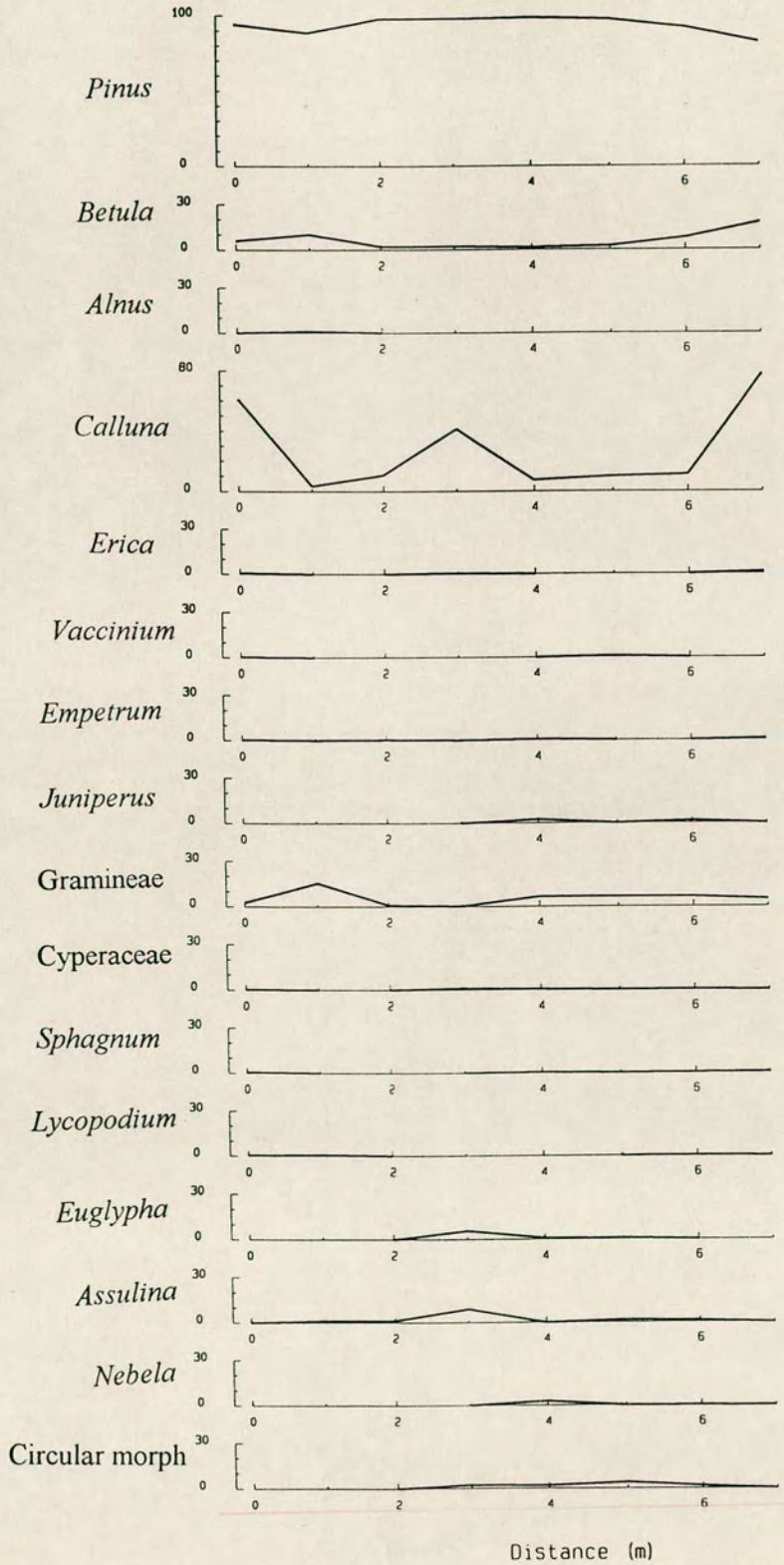
Table 6.4: Absolute pollen concentrations in thousands of grains per gram oven dry weight of moss polsters from modern pollen rain under *Juniperus* and *Calluna* at Creag Fhiaclach. For comparison, concentrations are also given for the heath surface samples at 707 m. (SE = standard error, n = 40, 16 and 5 for *Juniperus* canopy, *Calluna* canopy and the surface samples respectively, concentrations as 10^3).

		Pinus	*Betula*	*Calluna*	Gramineae	Cyperaceae
Juniperus canopy	mean	2,009	136	941	103	17
	SE	195	23	85	19	4
Calluna canopy	mean	1,886	411	10,155	518	79
	SE	273	111	1381	85	24
Surface at 707 m	mean	2,361	212	11,630	1,119	60
	SE	1,688	153	5,426	593	46

The standard errors on all the concentration figures were very large. Pollen concentrations in upland sites are usually very variable with large standard errors (Smith & Cloutman, 1988). Absolute pollen counts are affected by the growth rate, quality and density of the moss polster which increases the variability of the count. There is also a slight bias towards *Juniperus* quadrats being under forest and *Calluna* quadrats in the treeline or heath as described above in Section 6.2. Therefore no statistical inference was attempted from these data.

However, some trends do occur in the data. *Pinus* pollen concentration under the two canopy types and in the top section of the pollen cores are very similar. *Calluna* pollen was high in both the *Calluna* canopy polsters and in the surface samples, but an order of magnitude lower in the polsters from the *Juniperus* canopy. *Betula* concentrations are shown because *Betula* is assumed to be a regional pollen type. Concentration of *Betula*

Figure 6.1 a: Pollen assemblages immediately outside and through *Juniperus* patch one at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.



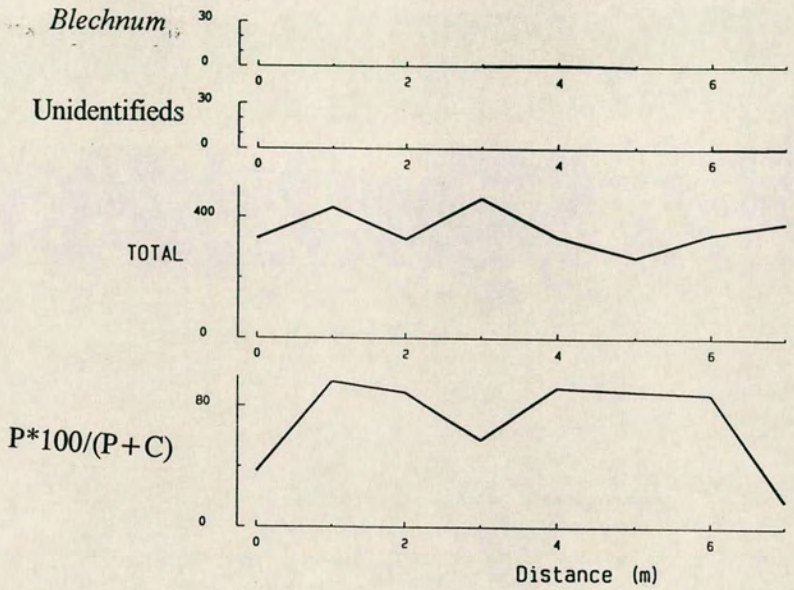
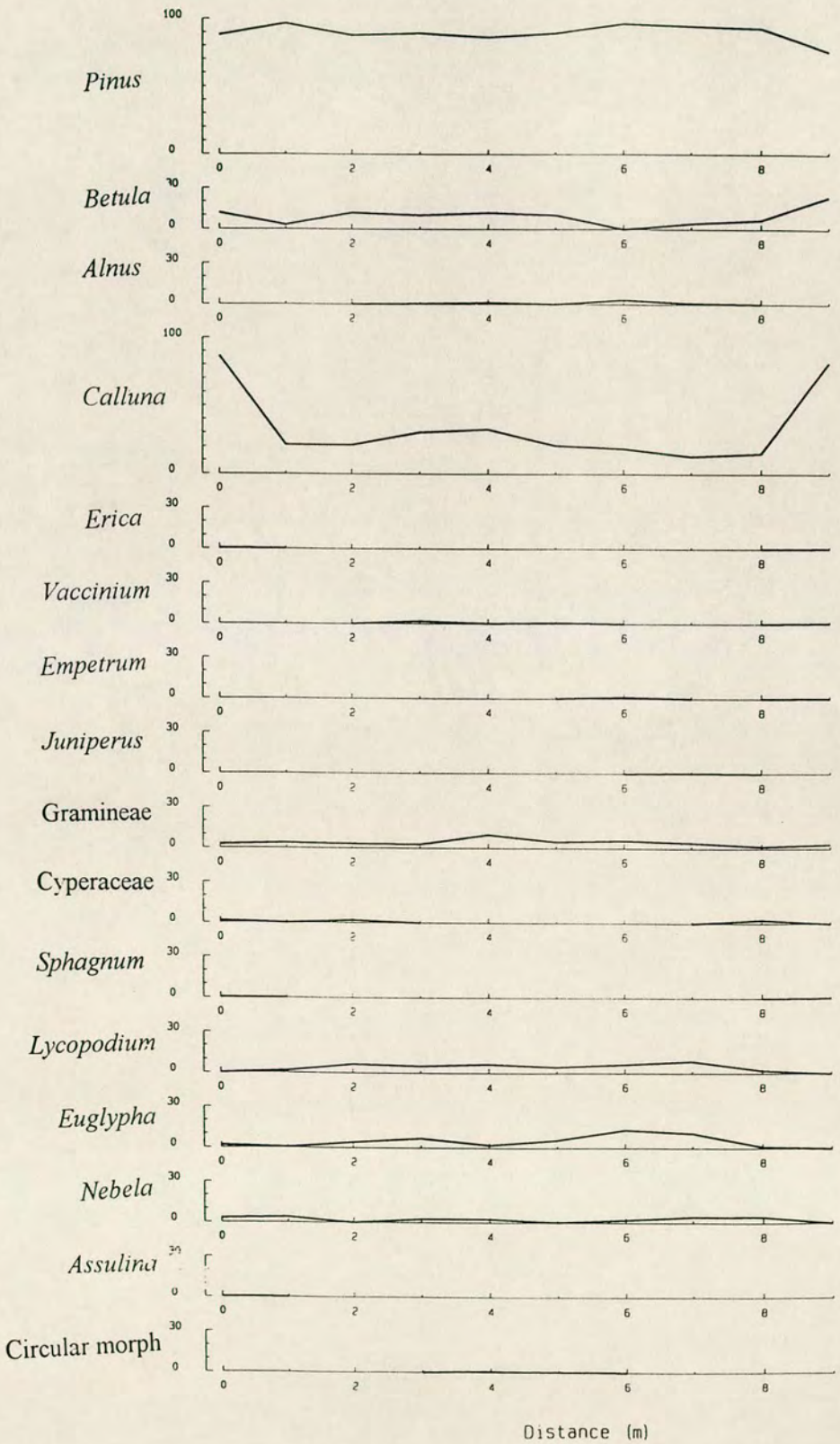

Blechnum
30
0
0
2
4
6
Unidentifieds
30
0
0
2
4
6
TOTAL
400
0
0
2
4
6
P*100/(P+C)
80
0
0
2
4
6
Distance (m)

Figure 6.1 b: Pollen assemblages immediately outside and through *Juniperus* patch two at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.



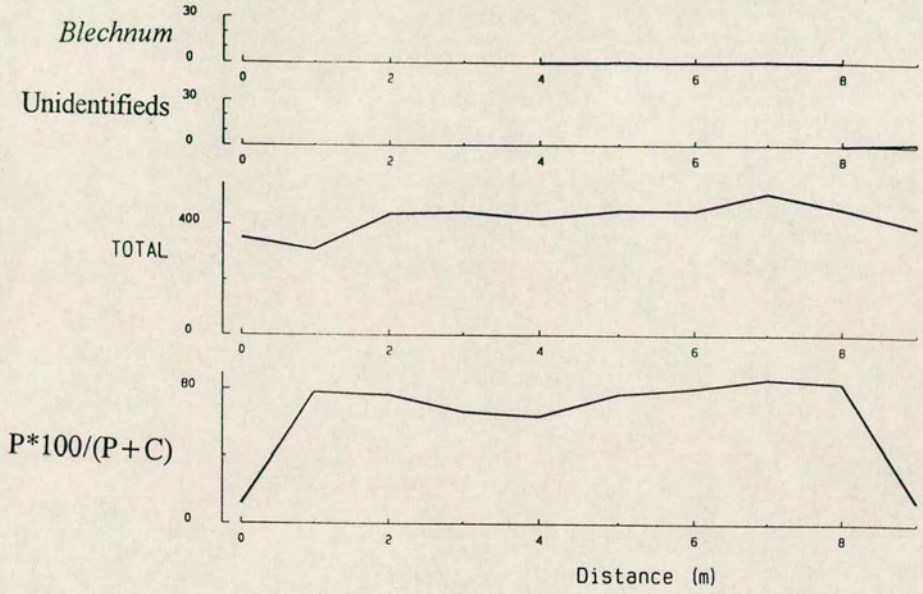
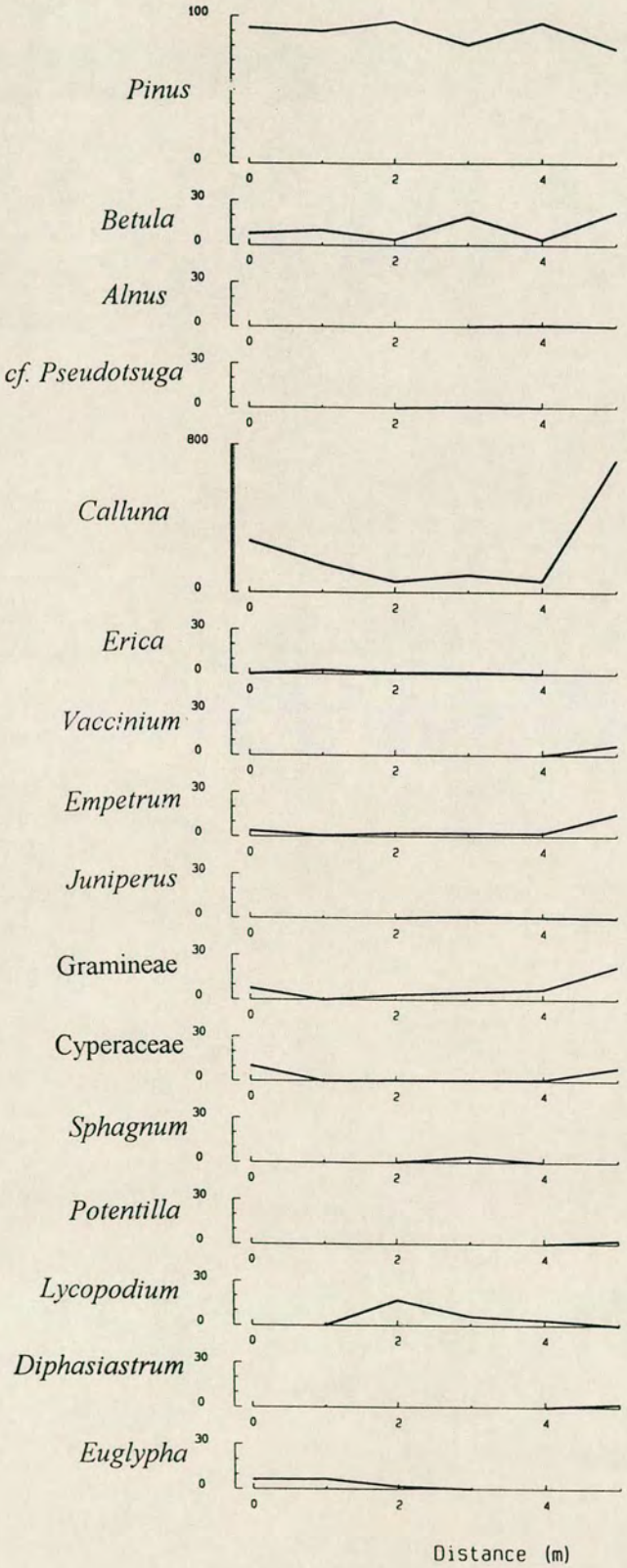

Blechnum
30
0
0
2
4
6
8
Unidentifieds
30
0
0
2
4
6
8
TOTAL
400
0
0
2
4
6
8
P*100/(P+C)
80
0
0
2
4
6
8
Distance (m)

Figure 6.1 c: Pollen assemblages immediately outside and through *Juniperus* patch three at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.



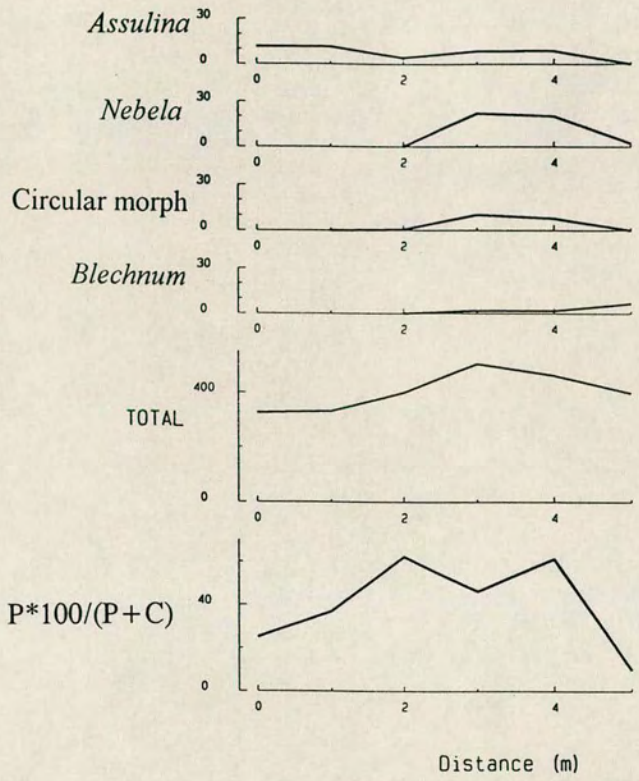
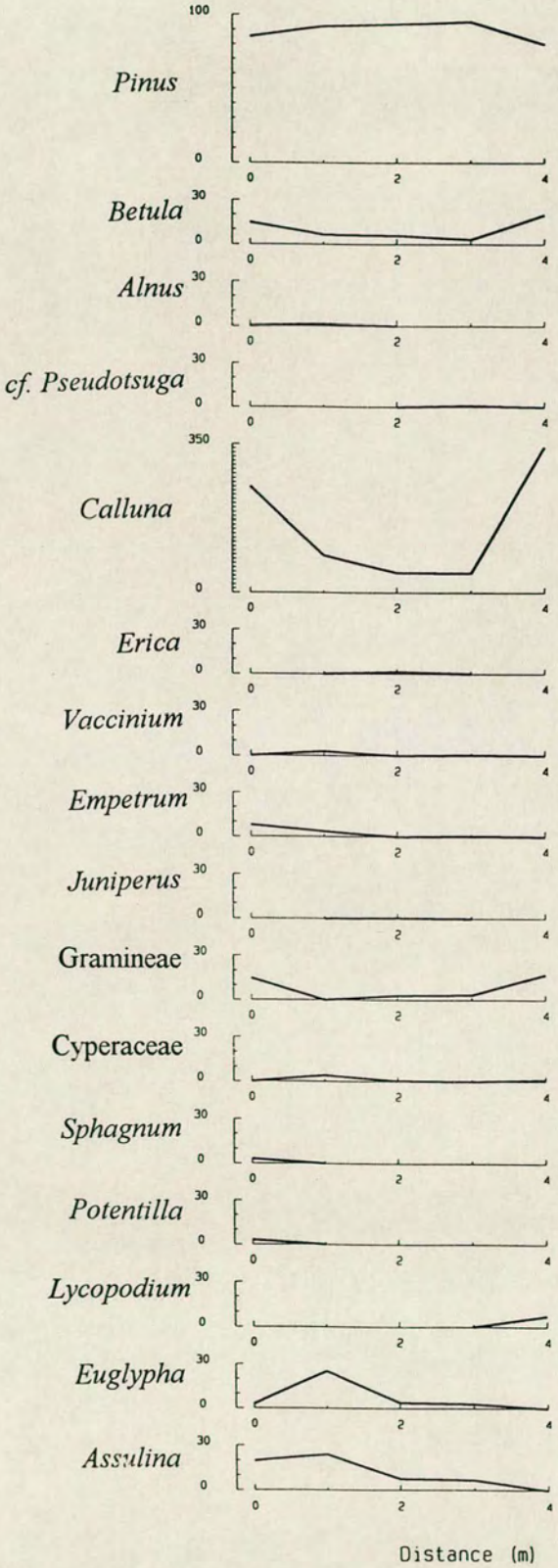

Assulina
30
0
Nebela
30
0
Circular morph
30
0
Blechnum
30
0
TOTAL
400
0
P*100/(P+C)
40
0
0
2
4
Distance (m)

Figure 6.1 d: Pollen assemblages immediately outside and through *Juniperus* patch four at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to



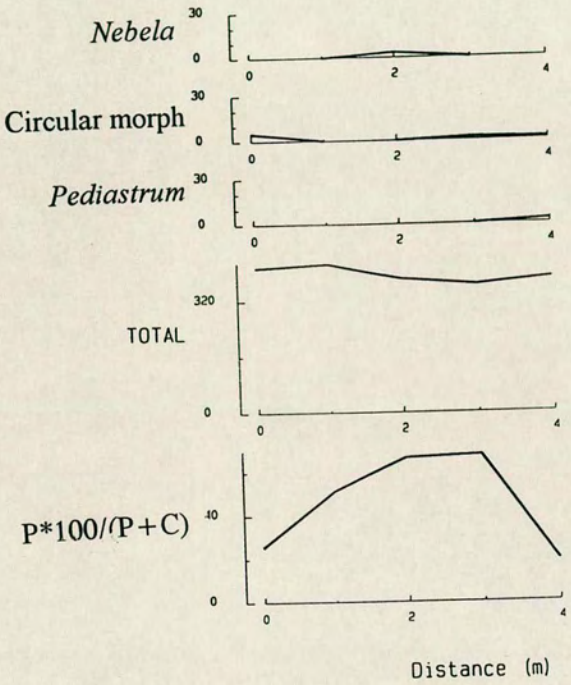
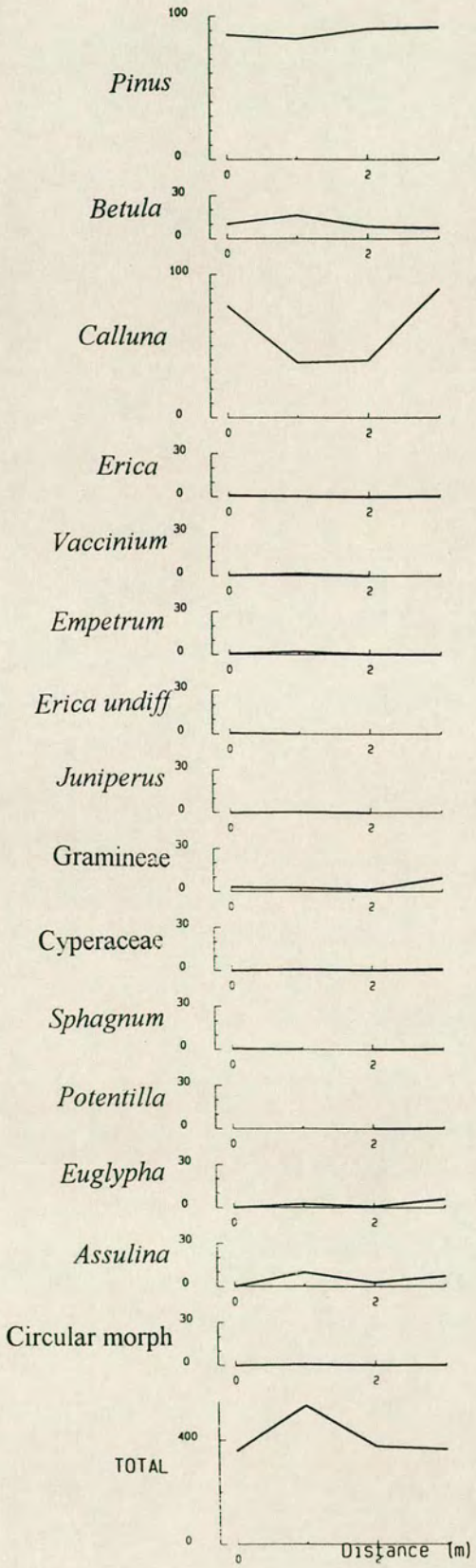

Nebela
30
0
0
2
4
Circular morph
30
0
0
2
4
Pediastrum
30
0
0
2
4
TOTAL
320
0
0
2
4
P*100/(P+C)
40
0
0
2
4
Distance (m)

Figure 6.1 e: Pollen assemblages immediately outside and through *Juniperus* patch five at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to



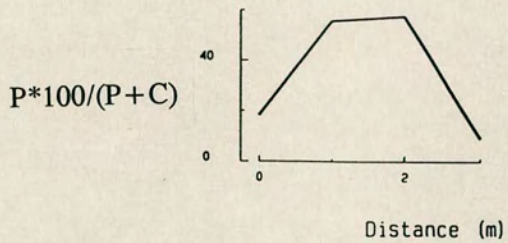
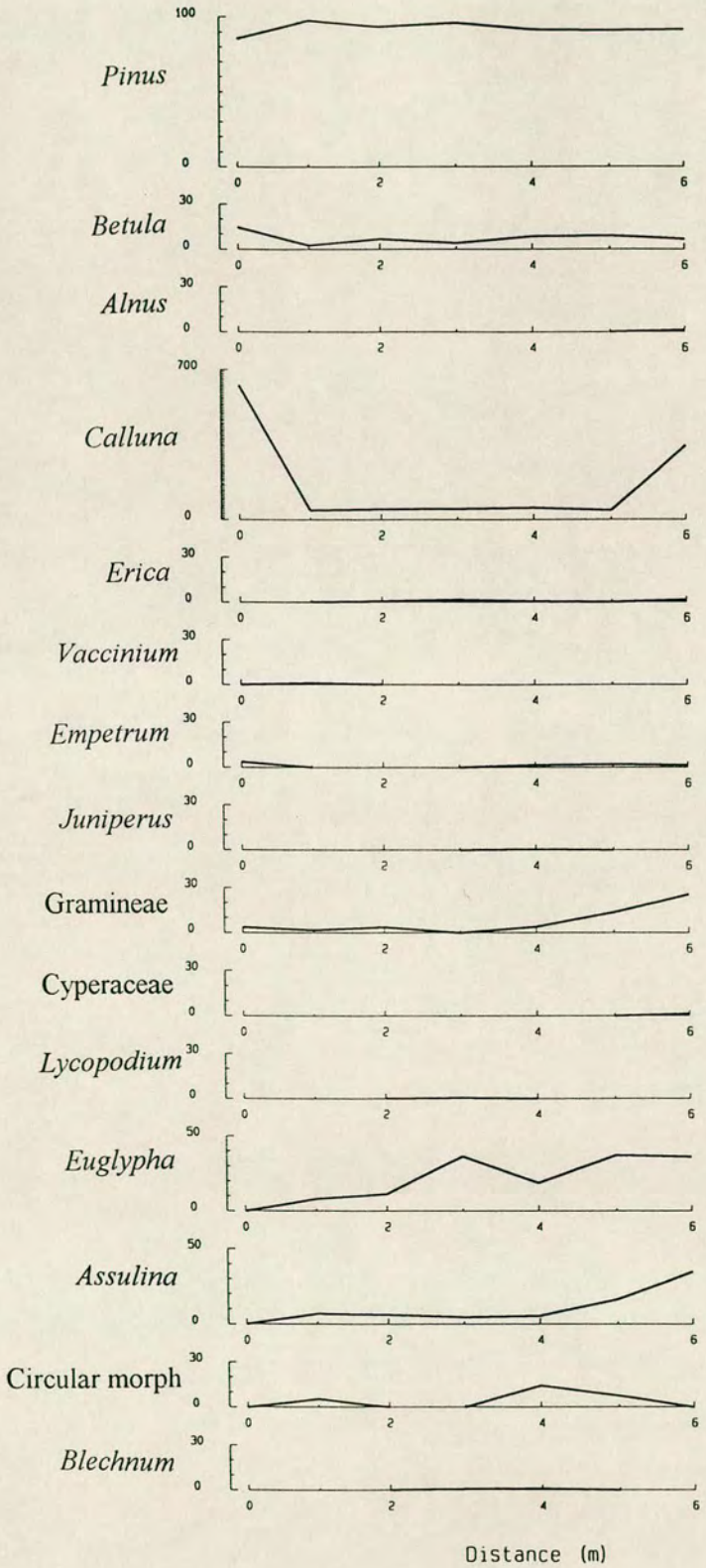

P*100/(P+C)
40
0
0
2
Distance (m)

Figure 6.1 f: Pollen assemblages immediately outside and through *Juniperus* patch six at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.



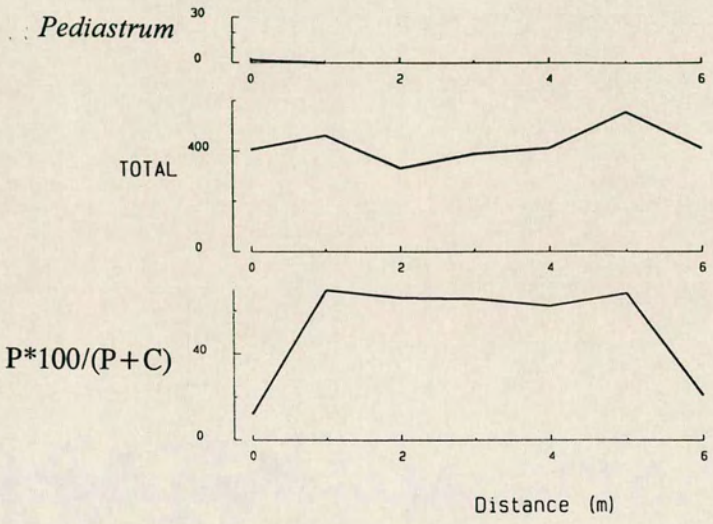
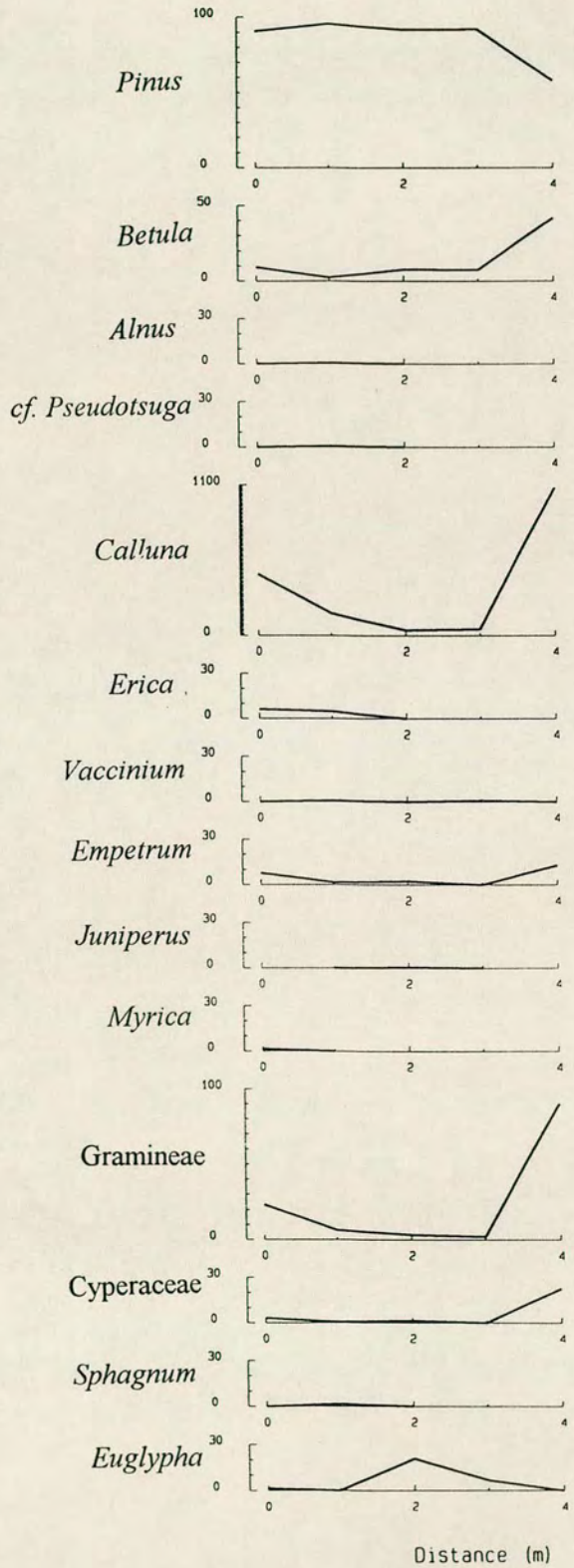

Pediastrum
30
0
0
2
4
6
TOTAL
400
0
0
2
4
6
P*100/(P+C)
40
0
0
2
4
6
Distance (m)

Figure 6.1 g: Pollen assemblages immediately outside and through *Juniperus* patch seven at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth.



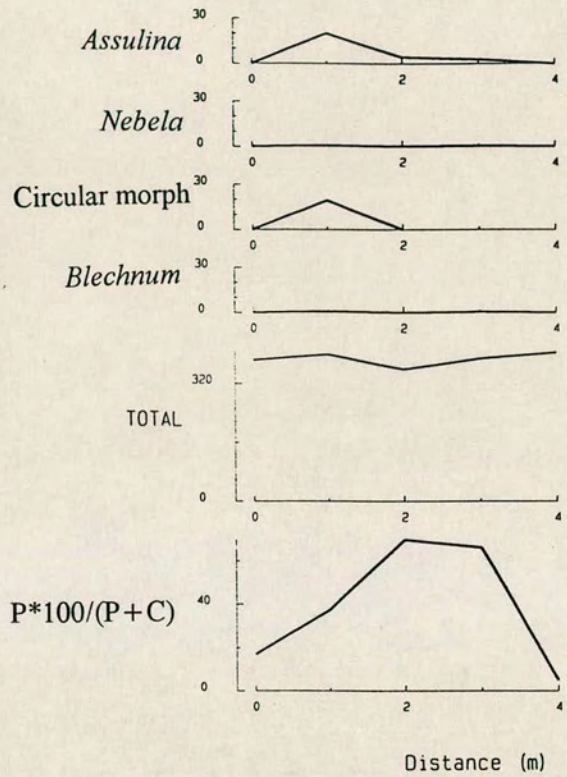
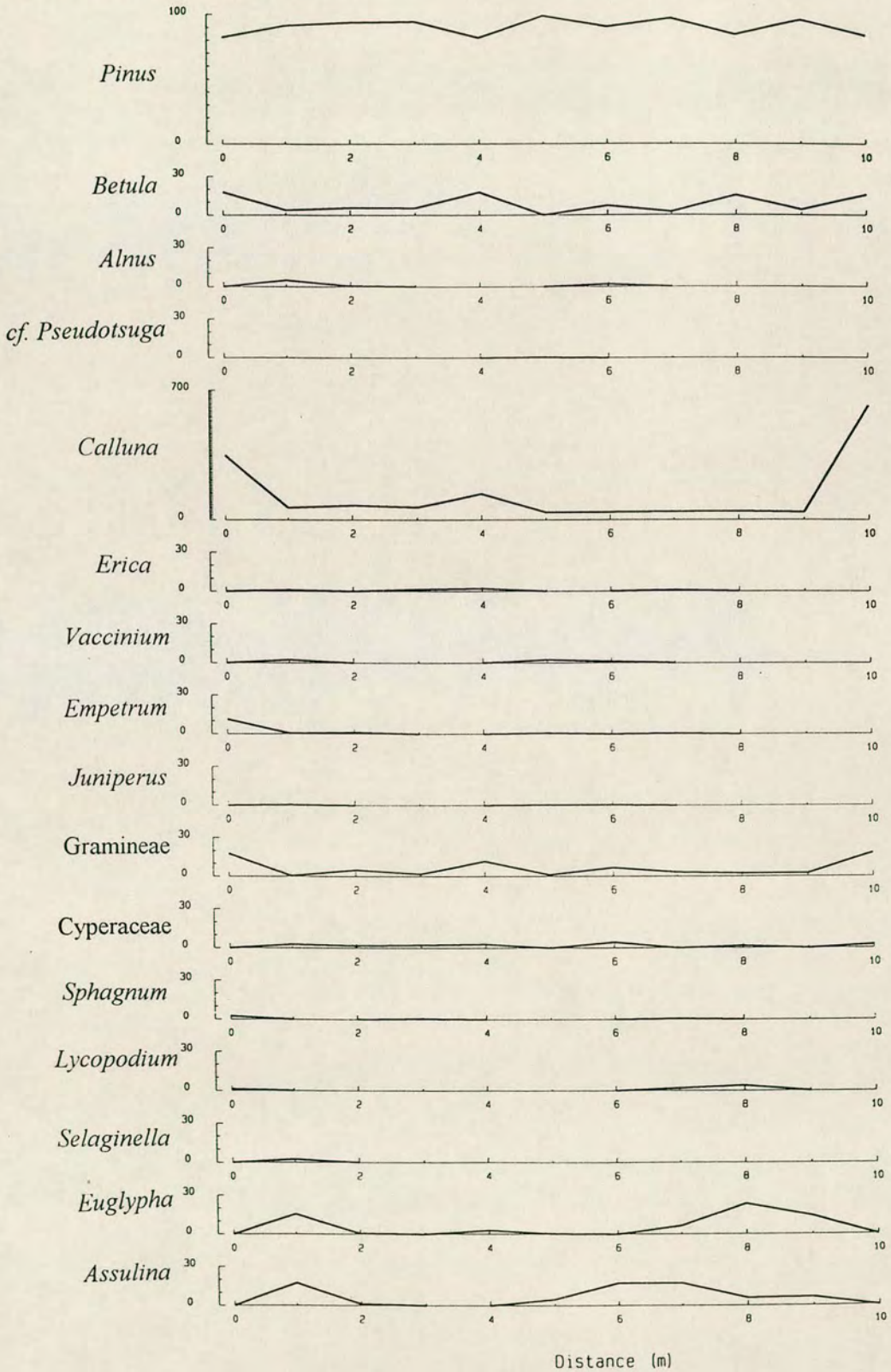

Assulina
30
0
0
2
4
Nebela
30
0
0
2
4
Circular morph
30
0
0
2
4
Blechnum
30
0
0
2
4
320
TOTAL
0
0
2
4
P*100/(P+C)
40
0
0
2
4
Distance (m)

Figure 6.1 h: Pollen assemblages immediately outside and through *Juniperus* patch eight at Creag Fhiaclach. Distance through patch is given on x axis. Scale on y axis gives percentages for the heavy black line. The lighter line depicts the representation of taxa under 5% exaggerated by a factor of ten. Horizontal bars are standard errors for up to five replicates for each depth



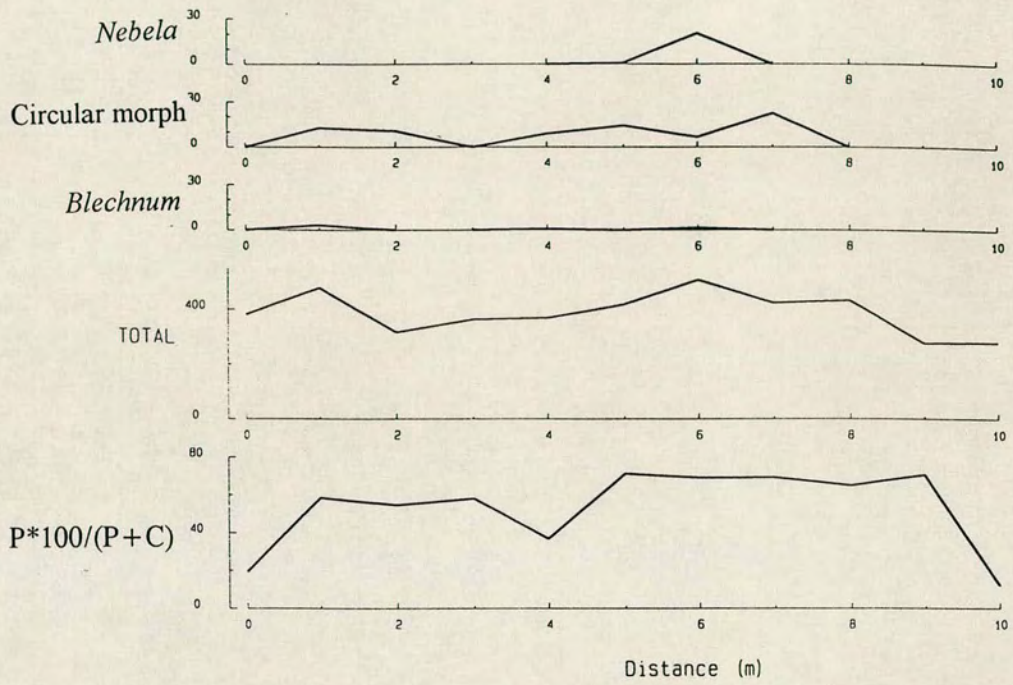
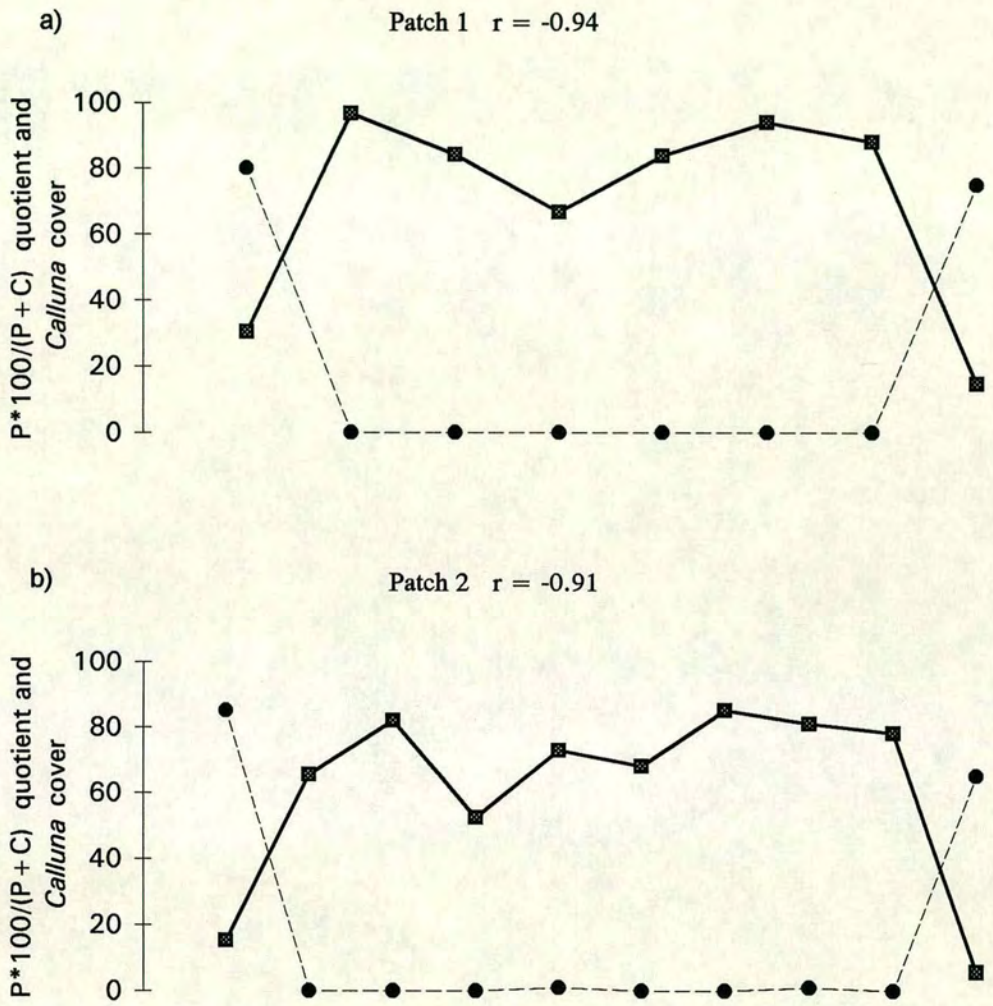
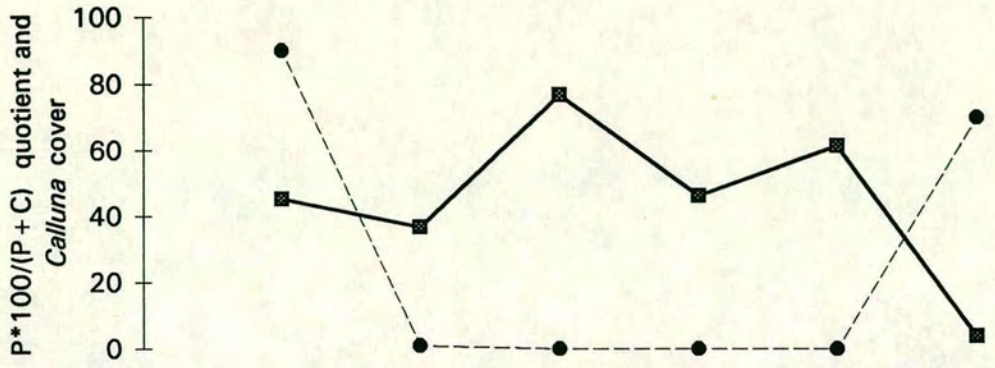

Nebela
30
0
Circular morph
30
0
Blechnum
30
0
TOTAL
400
0
P*100/(P+C)
80
40
0
0
2
4
6
8
10
Distance (m)

Figure 6.2 a-h: Percentage *Calluna* cover (filled circles) plotted with the change in the P*100/(P+C) quotient (hatched squares) across dense *Juniperus communis* patches of varying sizes at Creag Fhiaclach. The Pearson product-moment coefficient is also given.



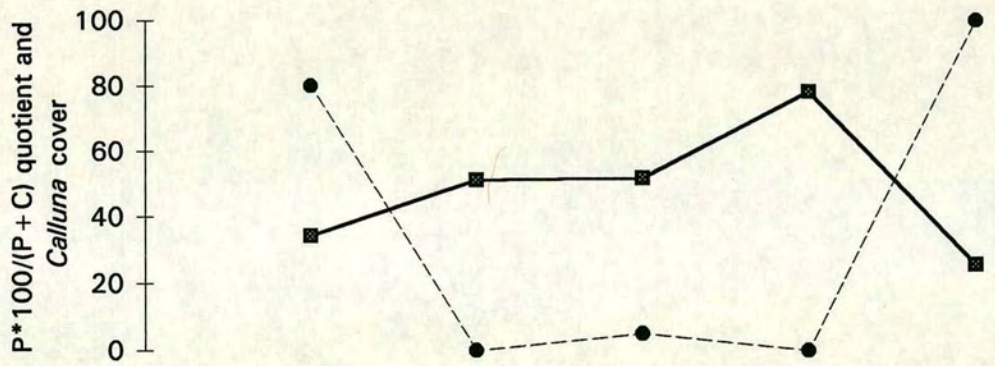
c)

Patch 3 r = -0.56



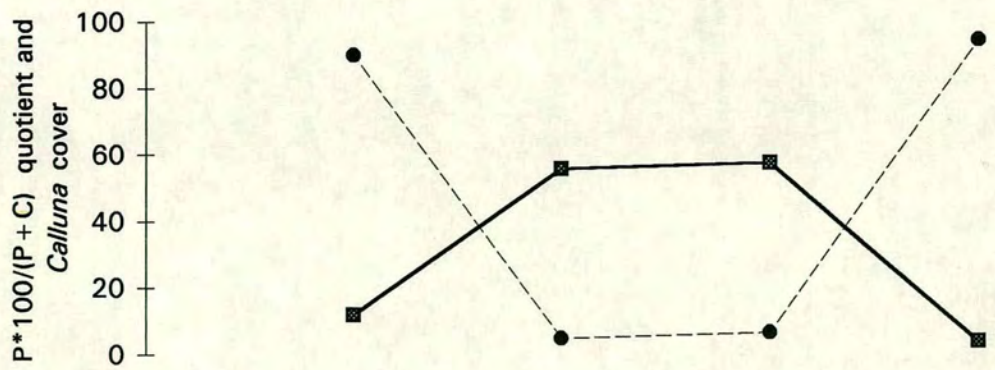
d)

Patch 4 r = -0.85



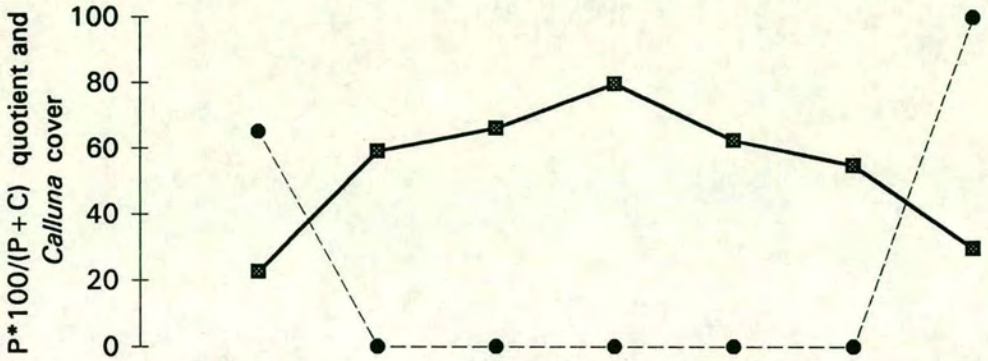
e)

Patch 5 r = -0.87



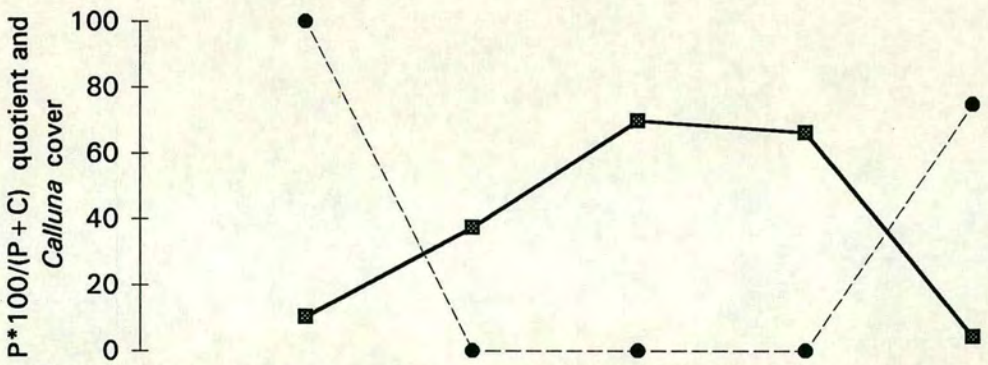
f)

Patch 6 r = -0.87



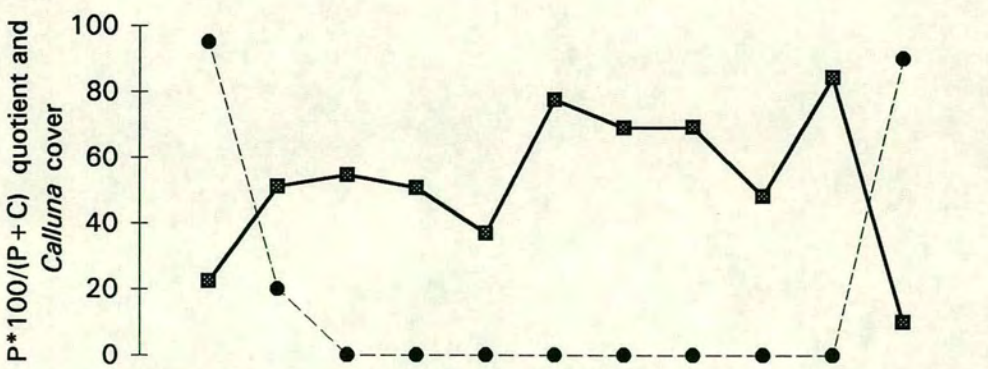
g)

Patch 7 r = -0.88



h)

Patch 8 r = -0.79



was twice as high in the *Calluna* canopy polsters as in the *Juniperus* polsters or surface samples. Pollen of Gramineae were at much lower concentrations in both of the canopy samples compared with the surface, and the concentration was much lower in *Juniperus* samples than *Calluna* samples. Concentration of Cyperaceae pollen was much lower in *Juniperus* polsters compared with *Calluna* polsters or surface samples, though as the actual number of grains counted were low the reliability of the concentrations must again be questioned.

6.4 Discussion

Dense *Juniperus* canopies cause changes in vegetation composition and pollen spectra. Vegetation under *Juniperus* had reduced contributions of *Calluna*, *Deschampsia flexuosa*, *Trichophorum cespitosum* and *Hylocomium splendens* (Table 6.2 and 6.3). Effects of shade on both the abundance and flowering of *Calluna* are discussed in Chapter 4. *Deschampsia flexuosa*, although generally shade tolerant shows reduced vigour and flowering under dense shade (Grime *et al.*, 1988). The response of *Hylocomium splendens* to shade has not been measured.

The reduction of *Calluna* in the vegetation was highly correlated with reduced *Calluna* pollen in the pollen spectrum (Figures 6.2 a-h). Although the absolute pollen concentrations had too much variation and too many assumptions for statistical inference they do indicate that the reduction in *Calluna* is a real reduction and not caused by increased concentrations of other taxa (Table 6.4). Conversely, *Pinus* pollen concentrations were fairly uniform. This would suggest that *Calluna* pollen released from the surrounding *Calluna* canopy is deposited very locally, with little pollen moving even 1 m into the adjacent *Juniperus* stands. Evans & Moore (1985) also found that there was a good correlation between representation and abundance of *Calluna,* indicating very local deposition. Meanwhile more regionally deposited pollen taxa such as *Pinus* are relatively unaffected by the species composition of shrub layer canopies. The concentrations of *Betula* and Gramineae pollen, which are also regionally distributed were ambiguous in this respect. This may be a reflection of the lower grain counts and errors associated with expression as concentrations. However, the notably lower pollen concentration of both Gramineae and Cyperaceae under *Juniperus* means that the second PCA axis in Chapter 5 may have been separating Gramineae/Cyperaceae flushes from '*Juniperus*' pollen spectra. The net effect of *Juniperus* canopies on the P*100/(P+C) pollen quotients is to produce quotients high in *Pinus* and more typical of forest-type pollen assemblages.

7

Chronologies

7.1 Introduction

Obtaining accurate and detailed chronologies for the past few millennia presents difficult problems for palynologists (Mannion, 1989a; b). These problems are compounded when working in upland peat which has a high spatial variation. In addition, the shallow nature of upland peats means that even minor instances of lateral transport can invalidate the results of chronological techniques. There are several highly technical approaches to dating presently available. These range from soot particle dating, which is useful for dating events around 1850-1900, but does not produce a strong signal, to technically advanced methods, such as accelerator mass spectrometry (AMS) radiocarbon dating which can use sample sizes so small that individual fractions of peat can be dated separately (Jones *et al.* 1989). In this chapter attempts to obtain chronologies for the peat deposit at Creag Fhiaclach are described. This is the highest peat deposit to be dated in the British Isles and possibly the only study of dating along an altitudinal gradient. The first technique is based on the temporal distribution of tephra, volcanic glass, and the other two techniques are radiometric (radiocarbon and ^{210}Pb). Radiometric dating can be very precise and establishes the age of peat deposits by measuring the content of specified isotopes.

7.2 Tephra Analysis

7.2.1 Introduction

Tephra is volcanic glass which is ejected high into the troposphere on a volcanic eruption. The volcanic glass is then later deposited on the land surface and can be incorporated into stratigraphic sediments forming an isochronous marker (Buckland *et al.*, 1981). The chemical composition of the tephra is unique in each eruption and by using an electon microprobe the chemical composition of deposited glass can be detected and the eruption from which it derived (Hunt & Hill, 1993). The eruptions themselves are dated from

historical records and other archaeological finds. Icelandic tephra has been deposited in Britain and Ireland at least seven times during the Holocene (Dugmore, 1989). The tephra layers most likely to be found in the Cairngorms are Hekla 4, Glen Garry and Hekla 1510 (A. Newton, pers. com.).

7.2.2 Laboratory Method

Two cores were collected from the treeline in addition to the cores for the palynological investigation at Creag Fhiaclach. These cores were split in two to provide material for testing the palynological procedures used in Chapter 5 and to provide material for tephra analysis. Wet acidic digestion was used to extract tephra, and the procedure was as follows. Two cm sections of peat from one sub-core were placed in a 200 ml conical flask. Sufficient concentrated sulphuric acid was added to cover the surface of the peat. This caused a violent reaction as the peat matrix had a high moisture content. When the initial reaction had subsided a few drops of concentrated nitric acid were added. If the mixture became effervescent at this stage a few drops of octan-2-ol were added. Once the reaction had stabilised, the flasks were transferred to a hot plate to keep the reaction going. Concentrated nitric acid was added at regular intervals, dropwise, until the reaction mixture stopped producing brown fumes of nitric oxides on addition of further nitric acid. At this point the reaction mixture was clear. After digestion, the samples were rinsed five or six times in distilled water. The supernatant was poured into running water. A plane polarising microscope was used to search for tephra shards as tephra can rotate plane polarised light and this distinguishes it from other minerogenic matter.

7.2.3 Results and Discussion

Only a few shards of tephra were found. There were insufficient numbers of shards to constitute a layer. The samples did however contain abundant numbers of diatoms. The presence of diatoms in the samples after digestion shows that the extraction technique was successful and that tephra has not been deposited in any quantity on this site.

7.3 Radiocarbon Dating

7.3.1 Introduction

^{14}C is produced when high energy neutrons from cosmic rays react with ^{14}N in the atmosphere. The ^{14}C which is produced rapidly reacts with O_2 to produce $^{14}CO_2$ which

is then photo-assimilated by living plants and subsequently may be assimilated by animals. When a plant or animal dies it stops assimilating carbon and the ^{14}C previously assimilated decays according to the first order decay equation. The extent of this decay is the basis of radiocarbon dating. The equilibrium activity of ^{14}C in living material is 13.56 dpm/gC (disintegrations per minute per gram of elemental carbon) which is equal to 0.226 Bq/gC. Thus, material with 6.78 dpm/gC has passed through one half-life and is 5730 years old.

This premise for radiocarbon dating assumes that the natural flux of radioactive CO_2 has been constant through time and that there are no other significant sources of radioactive CO_2. There are particular problems in dating the last few centuries. Extensive use of fossil fuels have reduced the specific activity of ^{14}C through dilution. H-bomb tests in the 1950s had the effect of doubling the specific activity of ^{14}C. Climatic fluctuations can also effect the size of the CO_2 reservoir. Because of these various fluctuations, radiocarbon years need to be calibrated into calendar years. Radiocarbon fluctuations have been calibrated by dating samples of known ages or through dendrochronology. Unfortunately, radiocarbon is particularly limited in its use to date events related to major climate changes as these periods tend to form plateaux in the calibration curves. The standard used for calibration is 95% of the activity in 1950 of the oxalic acid of wood from 1890, normalised to $^{13}C = -25‰$.

7.3.2 Methods

Samples for radiocarbon determinations were in two batches. The first batch was of an exploratory nature to ensure that useful data could be obtained from such a shallow deposit. For this run, samples were selected from the fourth replicate at 707 m as the palynological study suggested that this core could potentially indicate a higher elevation treeline in the past. The first sample from this core (4.25-5.25 cm) is just above the point where the P*100/(P+C) quotient changes from a heath to forest quotient. Unfortunately, this sample was enriched relative to modern and therefore a similar detailed analysis on replicate five at 707 m, which also showed a potentially higher treeline, was considered inappropriate at this point. Subsequently, further samples were analysed from replicate four to give a fuller picture of the chronology of the deposit. Differential accumulation rates of the peat deposit open the possibility that the bottom of replicates 1, 2 and 3 are

actually younger than that section of the deposit in replicate four where the pollen quotients switch from heath to forest assemblages. Hence, these deposits may be too young to have captured a treeline shift if one occurred. For this reason the end dates of these three cores and replicate five were determined. Three 5 mm samples, spanning the section of interest, were used for the radiocarbon determinations. This was sufficient peat to allow the synthesis of 1 g of benzene, the minimum quantity for the scintillation counter.

Peat samples were pre-treated before combustion. Peat has several components and pre-treatment means that various fractions of the peat can be dated. All obviously modern material was removed by spreading the peat on a watch glass and separating material with tweezers. To avoid underestimation, this method dated the humic fraction excluding roots. The fulvic acid fraction was removed in pre-treatment with HCl. The peat was heated in 150 ml of 1M HCl for two hours and left to cool overnight. The sample was then filtered using glass filter paper and vacuum suction after which the sample was put in an oven to dry. Peat samples were combusted and converted to acetylene via lithium carbide. The acetylene produced was subsequently converted to benzene by cyclotrimerisation using a chromium catalyst. Liquid scintillation counting took place after a period of three weeks, to allow for radon decay. The specific activity of the benzene was then determined using a high efficiency liquid scintillation counter at the Scottish Universities Reactor Research Centre at East Kilbride. In each sample, $\delta^{13}C$ was also determined to give an indication of the fractionation in both the biological fixing of carbon and chemical fractionation caused by the effect of the mass of ^{13}C on bonds. Incomplete combustion will enrich the sample in ^{13}C and deplete the CO_2.

7.3.3 Results

Table 7.1 contains the first set of radiocarbon dates and calibrated ages from replicate four at 707 m. Radiocarbon dates and calibrated ages for the subsequent set of samples are shown in Table 7.2. For ease of comparison, radiocarbon ages from all the samples are shown schematically in Figure 7.1.

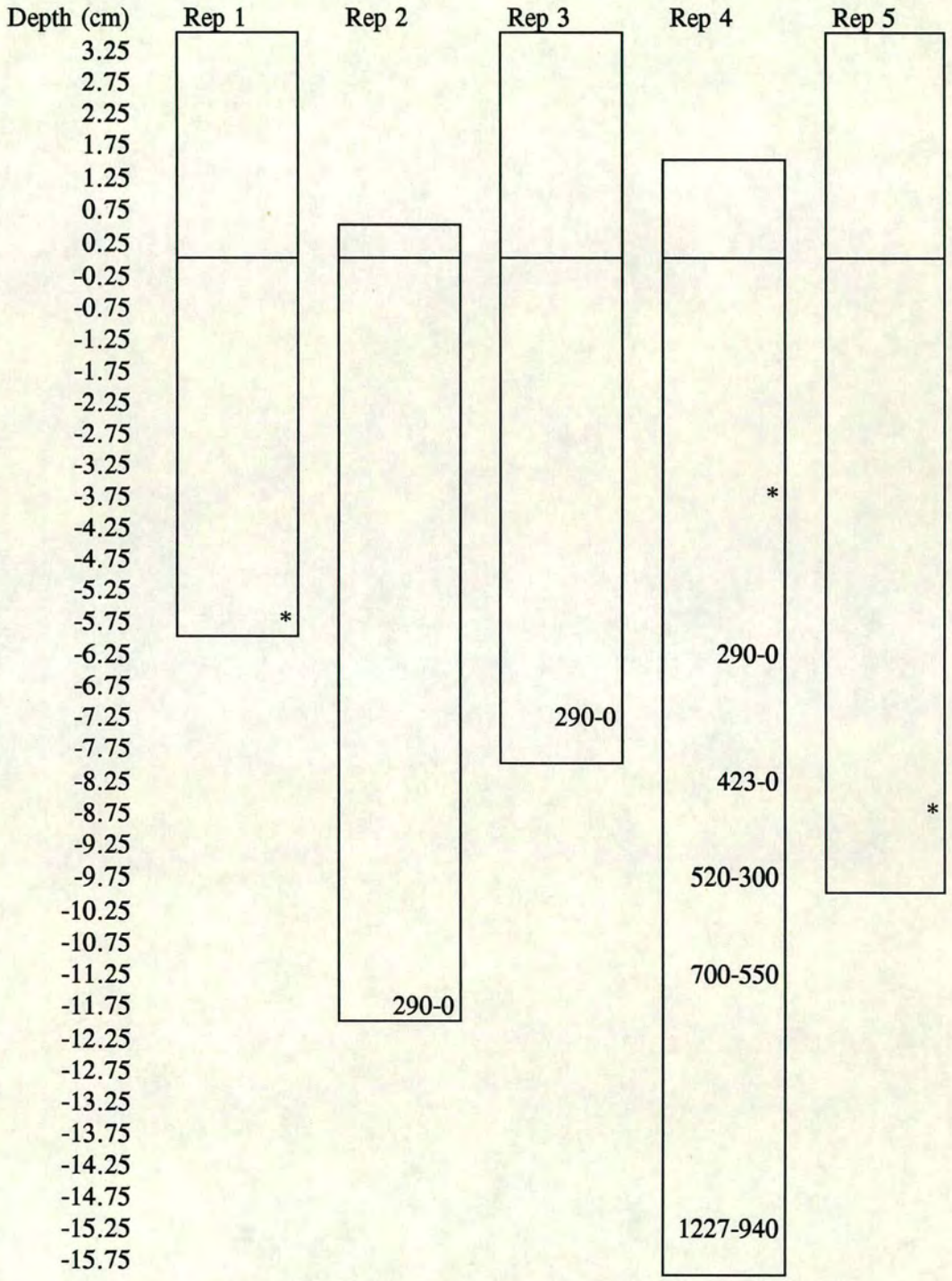
Table 7.1: Radiocarbon dates from selected depths in the fourth replicate above the treeline. Calibrated ages were determined at SURRC from the University of Washington, Quaternary Isotope Laboratory, Radiocarbon Dating Program, 1987. The 20 year atmospheric calibration curve was used throughout and the calendar age ranges, obtained from the intercepts (Method A), are expressed at both the one and two sigma levels of confidence. The $\delta^{13}C$ values for all the samples dated from Creag Fhiaclach are also given. Depth of midpoint is given in cm. * indicates the sample was outwith the range of calibration.

Lab number	Alt (m)/Rep	Depth		^{14}C age BP	Calibrated	$\delta^{13}C$
GU-3882	707 / 4	4.75	1σ	*		-28.7 °/oo
			2σ			
GU-3883	707 / 4	9.25	1σ	299-0	AD 1651-1955	-28.4 °/oo
			2σ	423-0	AD 1527-1950	
GU-3884	707 / 4	12.25	1σ	678-566	AD 1272-1384	-28.4 °/oo
			2σ	700-550	AD 1250-1400	
GU-3885	707 / 4	16.25	1σ	1140-975	AD 810-975	-28.8 °/oo
			2σ	1227-940	AD 723-1010	

Table 7.2: Subsequent radiocarbon dates. Calibrated ages were determined at SURRC from the University of Washington, Quaternary Isotope Laboratory, Radiocarbon Dating Program, 1987. The 20 year atmospheric calibration curve was used throughout and the calendar age ranges, obtained from the intercepts (Method A), are expressed at both the one and two sigma levels of confidence. The $\delta^{13}C$ values for all the samples dated from Creag Fhiaclach are also given. Depth of midpoint is given in cm. * indicates the sample was outwith the range of calibration.

Lab number	Alt (m)/Rep	Depth		^{14}C age BP	Calibrated	$\delta^{13}C$
GU-3985	707 / 4	10.75	1σ	502-320	AD 1448-1630	-28.8 °/oo
			2σ	520-300	AD 1430-1650	
GU-3986	707 / 4	7.25	1σ	271-0	AD 1679-1955	-29.3 °/oo
			2σ	290-0	AD 1660-1955	
GU-3987	707 / 3	10.25	1σ	268-0	AD 1682-1955	-28.6 °/oo
			2σ	290-0	AD 1660-1995	
GU-3988	707 / 2	12.25	1σ	263-0	AD 1687-1955	-28.5 °/oo
			2σ	290-0	AD 1660-1955	
GU-3989	707 / 1	9.00	1σ	*		-29.5 °/oo
			2σ			
GU-3990	707 / 5	8.50	1σ	*		-28.5 °/oo
			2σ			

Figure 7.1: Schematic diagram showing the distribution of radiocarbon determinations at 707 m at Creag Fhiaclach. Years as radiocarbon years BP. For ease of comparison, depths have been converted to the depths used to plot the pollen diagrams and the core outlines are aligned to the boundary between unconsolidated and consolidated peat. This boundary is shown as a horizontal line. * indicates the sample was outwith the range of calibration.



7.3.4 Discussion

Considerable overlap in the calibrated dates of replicate four at 707 m, when considered at 2σ, indicates that ^{14}C dating as used here is unable to date with precision the uppermost sections of the peat profiles.

Peats in the Cairngorms are very slow growing (Pears, 1975b) and there is a considerable stratigraphic variation in the shallow peats at this site (Chapter 2). This complicates radiocarbon dating. In shallow deposits there is a danger of underestimation of age and loss of resolution in ageing deposits because of the presence of roots. Although all obviously modern material was removed from the Creag Fhiaclach samples before dating, very fine roots are difficult to remove. An over-estimation can occur through solifluction and inwashing of older material. The presence of stratified mineral layers in the X-radiographs (Figure 7.2 a-d) shows that solifluction may have been common in the early stages of peat formation, but not recently. Hence the error from solifluction at Creag Fhiaclach will be minimal because in the early stages of peat formation, soliflution will have deposited material which is of approximately the same age as the deposit. Contamination through inwashing of older material through the peat matrix is a more likely source of error. However, in light of the sample from replicate two having a radiocarbon signal which was enriched relative to modern at -11.75 cm, and thus had an unlikely accumulation rate of approximately 0.25 cm y^{-1}, it is more probable that the radiocarbon dates are an under-estimation of the actual ages of the deposit. The radiocarbon base dates cannot give a precise date for peat initiation on the site as the radiocarbon dates calibrate to a wide range. Unfortunately the section of most interest at -3.75 cm was enriched in ^{14}C relative to modern. Therefore estimation of a date for this section was not possible. The end dates of the other cores were all either enriched relative to modern or modern. Within the range of error in the dates it is thus theoretically possible that the ends of these cores are younger than the point in replicate four where there is a change in the pollen quotients. In conclusion, while the radiocarbon dates show stratigraphic validity, the quantity of modern material in the surface layers and the shallow nature of the deposit severely restrict temporal resolution.

7.4 ^{210}Pb Dating

7.4.1 Introduction

The disadvantages of radiocarbon dating, i.e., the standard error of the radiocarbon age, problems of calibration and the quantities of peat required, become very serious when dating samples that are only a few hundred years old. Recent advances in radiocarbon dating techniques have resolved the problem of sample size. However, the problems

associated with calibration remain. The shallow nature of the peat at Creag Fhiaclach may also limit the use of radiocarbon. In recent decades other radiometric techniques have been developed. Of these ^{210}Pb, which was first proposed by Goldberg (1963), shows most promise for dating the last two centuries. ^{210}Pb is a product in the uranium decay series and is ideal for dating the last two hundred years as the half life is 22.26 ± 0.22 years. After two hundred years the activity is low and difficult to measure.

Virtually all geological strata contain limited quantities of uranium. The product in the decay series which enables ^{210}Pb to be used for dating is radon gas. When formed, radon gas escapes from the geosphere and is circulated in the atmosphere. Radon gas decays rapidly through to ^{210}Pb in the atmosphere and as a solid is subsequently deposited and incorporated into stratigraphic sediments. Sediments can then be dated on the basis of net retention of ^{210}Pb.

The main question is, under what circumstances can a ^{210}Pb assay be regarded as a reliable dating technique for upland peat? ^{210}Pb dating has really been developed for dating lake sediments and as yet is not a widely used method for peat (El-Daously *et al.*, 1982). This is despite the fact that peats should be easier deposits to date because of their low mineral content. There are two fundamental assumptions in ^{210}Pb dating. Firstly, that the lead being counted is unsupported and secondly, that there is perfect retention of the lead once it enters the peat matrix. ^{210}Pb derived from atmospheric sources alone is called the unsupported ^{210}Pb. Where there is a continuous supply to all depths from ^{222}Rn decay within each layer this is termed the supported ^{210}Pb. This may well be present at Creag Fhiaclach as the underlying rock is granite which contains uranium. The contribution of supported lead can be estimated from the radium activity.

Of these two assumptions, that of perfect retention is most questionable. Lead can become mobile in saturated peats with fluctuations in oxidation/reduction conditions around the region of the water table causing most problems (Damman, 1978). Evidence has shown that ^{210}Pb underestimates age when compared with growth increments of *Sphagnum* and *Polytrichum* for continental bogs (El-Daously *et al.*, 1982). The ^{210}Pb tends to move slightly down the profile due to water movements. Errors caused by movement of lead can be estimated by measuring the peaks in concentration of ^{137}Cs and ^{241}Am, neither of which occurs naturally, but were produced by nuclear weapons tests with peak concentrations in 1963. Weapons testing in the 1950s and 1960s resulted in the deposition of 1900 Bq/m^2 of ^{137}Cs while the accidental release from the Chernobyl reprocessing plant resulted in a further 1000-10000 Bq/m^2 being deposited (Santschi & Honeyman,

1989). ^{137}Cs has a half life of 30.23 yr. and the Chernobyl flux should still be readily detectable. Often the ^{137}Cs profile is not suitable in peat deposits as ^{137}Cs can be absorbed and metabolised as potassium in plants.

7.4.2 Field Methods

In addition to the thirty cores for pollen analysis, six monoliths 20 cm x 20 cm to a depth of 25 cm were extracted for ^{210}Pb dating in July 1993. The monoliths were collected as two replicates from three altitudes spaced 100 m apart along the ground. Replicates were 100 m apart along the contour. The highest altitude was above the tree-line, second was at the tree-line and the lowest altitude was within the *Pinus* canopy. An additional core was collected from the treeline in April 1994 for high resolution analysis. Cores were wrapped in plastic and stored at 4 ^{o}C.

7.4.3 Sample preparation

Before sectioning, the six cores collected initially, were X-rayed to ensure the stratigraphy was horizontal (Dugmore & Newton, 1992). X-rays were taken of 2 cm thick slices using a SCANRAY 120L machine at the British Geological Survey in Edinburgh. The machine was operated with a potential of 35 kV, an acceleration current of 2 nA and exposure time of 90 s. Prints of the X-rays (Figure 7.2 a-d) show layers of minerogenic material towards the bottom half of the cores. These layers are associated with solifluction events in the early stages of peat formation on the site. The most important feature of the layers is that they are all horizontal. Cores were then sectioned into 3 cm slices. Wet volumes were noted and sections weighed before being dried in an oven at 80 ^{o}C until no further weight change occurred. They were then re-weighed to calculate moisture content and bulk density. Samples were subsequently homogenised in a coffee grinder. A sample of 15 g was then pelleted to a depth of 1.5 mm using a hydraulic press to apply a pressure of 1.5 tonnes. The pellets were then re-weighed to four decimal places and wrapped in cling-film (polyvinyl chloride). Samples were pelleted from the bottom of the core to the top to reduce contamination errors. Preparation for the high resolution core was similar, except that the core was sectioned into 0.5 cm slices and roots were removed from these before grinding. The ^{210}Pb activity of the roots was determined separately.

7.4.4 Gamma Spectrometry

Nature of Gamma Radiation

Nuclear transition from higher energy states to lower energy or ground states in radionuclides such as ^{210}Pb, ^{226}Ra and ^{137}Cs involves the release of gamma rays. Gamma rays can interact with matter via the photoelectric effect, Compton scattering or

pair production. The probability of the photoelectric effect occurring is related to $E^{-7/2}$ at low energies and to 1/E at higher energies (E) of the gamma ray. Photoelectric events have characteristic energies for distinct disintegrations from different elements. Measurement of photoelectric peaks at different energies can be used to identify the radionuclides while the areas under the peaks can give an estimation of the quantity of the radionuclides present. Compton scattering occurs when gamma photons are scattered with reduced energy. The probability of Compton scattering is related to the number of electrons in the atom and is hence proportional to Z (path length from sample to detector) and is inversely proportional to gamma energy. The Compton effect gives a continuum of scattered gamma ray energies.

Principles of Gamma Radiation Detection

Gamma spectra were recorded using a germanium (Ge) gamma photon detector. Ge is a semiconductor which, if cooled to liquid nitrogen temperatures is an electrical insulator. Under these conditions, if a potential difference is applied to a Ge crystal no current will flow. If radiation photons enter the crystal they will cause ionisation giving small electrical pulses, the sizes of which are proportional to the photon energies. Measurement of each pulse constitutes the basis of gamma spectropy.

The Germanium Detector

Direct gamma assay allows simultaneous measurement of all gamma emitting radionuclides (Appleby *et al.*, 1986). The gamma emission spectra of the Creag Fhiaclach peat deposits were determined using a Canberra high-purity, n-type, planar, low background Ge detector, with a 0.55 mm epoxy resin window. The germanium crystal was 43.7 mm x 43.7 mm x 15 mm. Full width at half maximum (FWHM) resolution of this system was 0.346 keV at 5.9 keV and 0.605 keV at 122 keV. The detector is operated at 77 ^{o}K, in liquid nitrogen, as normal room temperatures are sufficient to promote electrons to the conducting band. Pulses from the detector passed through an amplifier and an Ortec 918 multi-channel buffer before compilation in an IBM compatible PC.

Peaks were subsequently detected and analysed using an Ortec minigam 2 program. The area under the photopeaks gives the count rate as counts per second. To calculate the absolute concentration of a given nuclide from the counts per second the value must be multiplied by a factor which takes account of the detection efficiency.

Calibration

The radiation detection efficiency was calibrated using standard solutions of the radionuclide of interest. For the peats from Creag Fhiaclach standard pellets were made using homogenised material from the lowest layer which is unlikely to contain any ^{210}Pb. Solutions of known ^{210}Pb, ^{137}Cs and ^{226}Ra content were added dropwise to the pelleted standards and allowed to dry. A calibration curve was calculated from these. Absolute efficiencies are given in Table 7.3.

Table 7.3: Detection efficiencies for different nuclides at different pellet weights.

Pellet weight	^{210}Pb	^{226}Ra	^{137}Cs
5 g	0.65	1.10	2.65
10 g	0.58	1.14	2.47

7.4.5 Lead accumulation curves

Results of the gamma spectrometry of peat samples from Creag Fhiaclach are given in Tables 7.4 and 7.5. ^{210}Pb was detectable in all the peat samples. However, no ^{210}Pb was recorded in the roots, separated from the peat matrix in the high resolution core.

Table 7.4: Summary of nuclides of interest recorded from six peat cores collected from Creag Fhiaclach. Measurements are given as Bq kg^{-1} with one standard deviation of uncertainty. Two peaks are given for ^{226}Ra. Laboratory codes are montane (m), treeline (t) and woodland (w). The first digit is the replicate and the last digit is the depth number. BDL signifies below the detection limit of the system. Depth of midpoint given in cm.

Lab code	Depth	^{210}Pb	^{226}Ra (238)	^{226}Ra (352)	^{134}Cs	^{137}Cs
m11	-1.5	626±13	21±1	19±3	15±2	509±6
m12	-4.5	323±13	33±2	28±4	BDL	352±7
m13	-7.5	222±15	60±2	80±3	BDL	46±4
m14	-10.5	121±10	70±2	47±3	BDL	33±4
m21	-1.5	343±10	4±1	11±3	18±3	254±8
m22	-4.5	283±11	2±1	15±4	BDL	131±5
m23	-7.5	198±8	14±2	48±4	BDL	42±3
m24	-10.5	131±11	23±2	44±4	BDL	53±4
m25	-13.5	123±11	37±2	41±3	BDL	47±7
m26	-16.5	97±7	47±2	47±3	BDL	23±3
t11	-1.5	364±15	6±2	BDL	41±5	509±10
t12	-4.5	242±7	4±1	6±2	11±3	182±4
t13	-7.5	123±7	4±1	16±4	BDL	41±4
t14	-10.5	93±9	15±2	32±3	BDL	70±5
t21	-1.5	343±8	BDL	11±4	16±2	655±8
t22	-4.5	323±10	BDL	BDL	BDL	250±7
t23	-7.5	242±7	BDL	8±2	BDL	133±5
t24	-10.5	107±5	4±1	13±4	BDL	57±4
t25	-13.5	32±4	9±2	2±1	BDL	40±4
t26	-16.5	32±4	1±0.2	10±2	BDL	32±2
w11	-1.5	465±14	8±2	10±3	61±5	752±15
w12	-4.5	210±8	3±1	12±3	BDL	92±5
w13	-7.5	77±12	36±2	24±3	BDL	48±5
w21	-1.5	323±13	6±1	BDL	39±5	511±10
w22	-4.5	303±10	12±2	27±3	BDL	72±4
w23	-7.5	133±11	29±2	56±5	BDL	182±7

Table 7.5: Summary of ^{210}Pb, unsupported ^{210}Pb (XS ^{210}Pb) and ^{137}Cs in the high resolution core. Concentrations are in Bq kg^{-1} and the uncertainty at one standard deviation is given in the adjacent column.

Depth (cm)	^{210}Pb	1σ	XS ^{210}Pb	1σ	^{137}Cs	1σ
-0.25	468	22	448	22	386	5
-0.75	491	23	473	23	304	5
-1.25	453	28	430	28	161	3
-2.25	320	14	314	14	100	2
-2.75	307	25	303	25	104	3
-3.25	224	17	203	18	103	3
-3.75	218	11	210	11	95	2
-4.25	216	10	202	11	104	2
-4.75	148	9	158	10	97	2
-5.25	119	9	102	11	87	2
-5.75	123	16	99	17	50	2
-6.25	98	16	78	16	76	2
-6.75	92	11	70	13	72	2
-7.25	136	24	100	27	85	2
-7.75	138	20	107	23	66	2
-8.25	119	15	91	16	60	2
-8.75	136	11	109	11	56	2
-9.25	157	13	132	14	45	2
-9.75	137	16	101	18	46	2
-10.25	107	14	76	15	46	2
-10.75	134	15	87	16	41	2
-11.25	85	11	40	12	25	2
-11.75	431	18	421	19	119	3

Lead accumulation curves were calculated for both the six altitudinal cores and for the high resolution core. The data were first corrected for the presence of supported ^{210}Pb which was estimated from the ^{226}Ra concentration. The quantity of radium present was calculated from the two peaks of ^{214}Bi, a descendant of ^{216}Ra, as ^{216}Ra has a peak at 186 keV as ^{235}V also has a gamma emission at this energy. The estimated ^{226}Ra count was then subtracted from the ^{210}Pb count to give a net unsupported ^{210}Pb count. In accordance with the radioactive decay law, unsupported ^{210}Pb counts should decline with increasing age of the sediment. Unsupported lead concentrations as functions of depth are given in Figures 7.3 and 7.4.

Figure 7.3 a-f: Logarithm of unsupported ^{210}Pb accumulation curves from the three altitudes at Creag Fhiaclach, spanning the treeline.

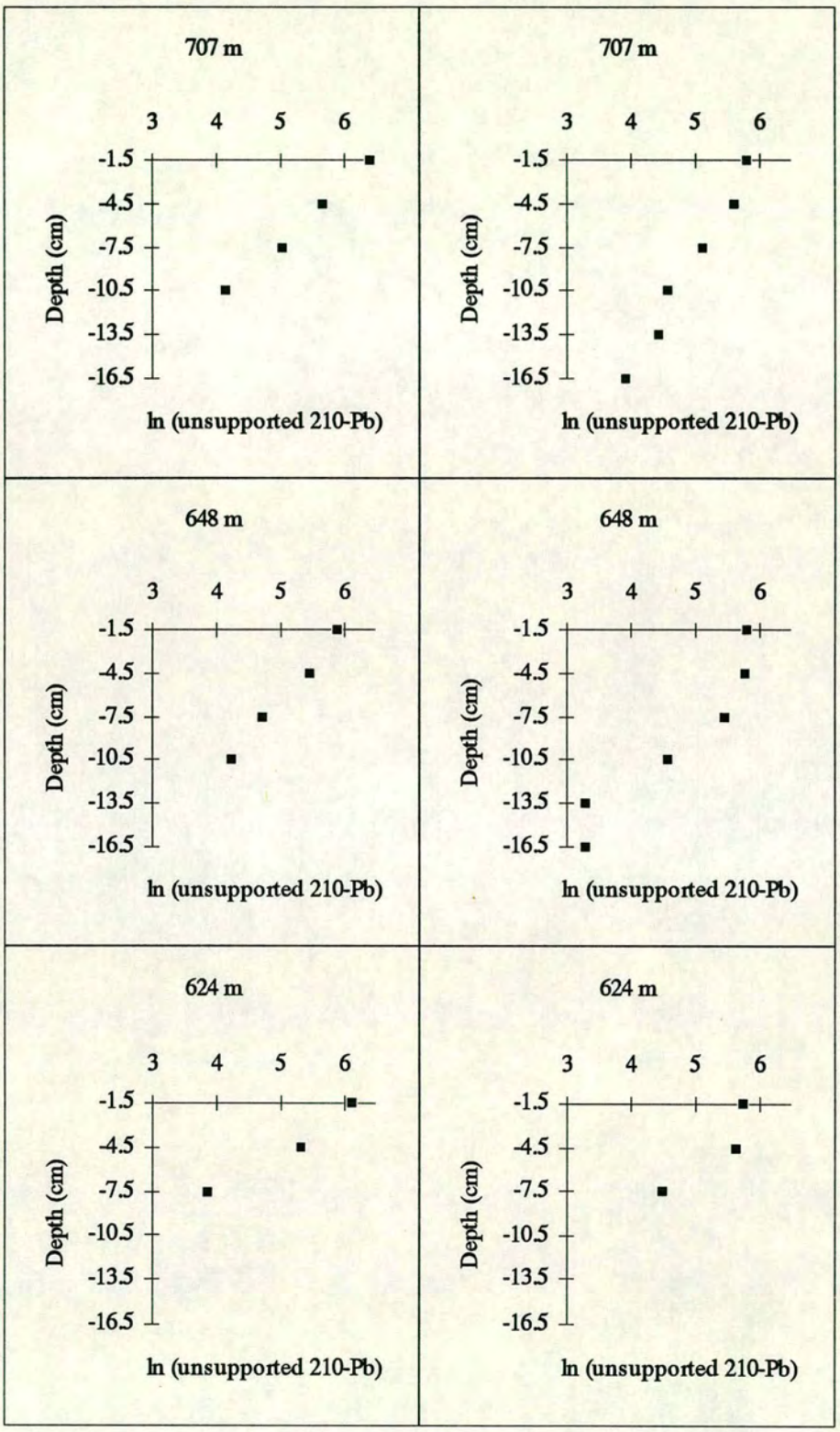
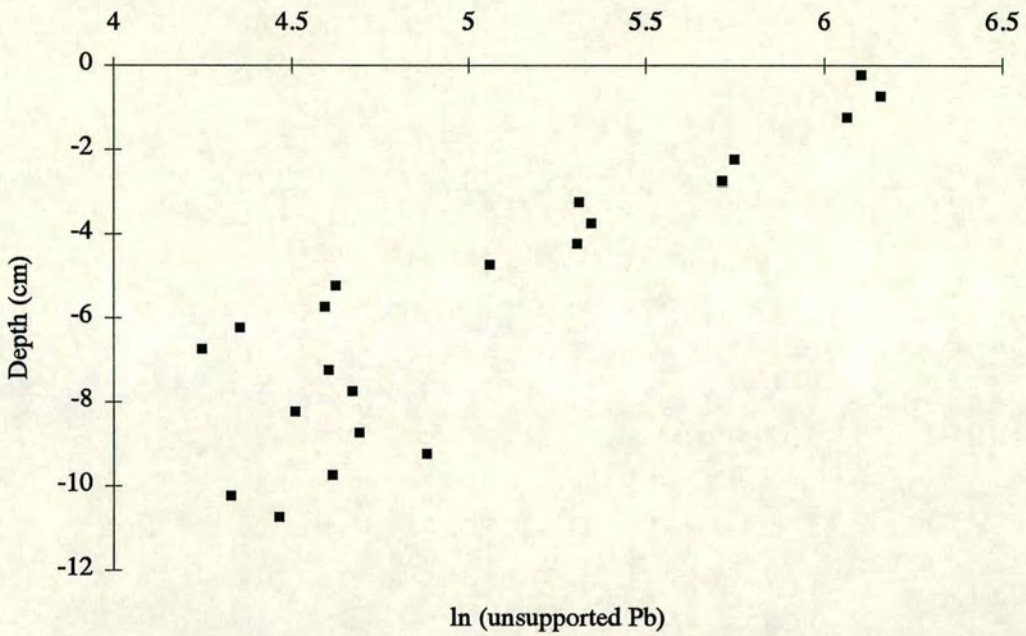


Figure 7.4: Logarithm of unsupported ^{210}Pb accumulation curve for the high resolution core at Creag Fhiaclach.



All of the curves show a decrease in the ^{210}Pb concentration with depth. Sediment accumulation rates were determined from the mean slope of the graphs, Table 7.6. This method of determining sedimentation rate is adequate in a deposit where the rate of sedimentation is relatively constant (Appleby & Oldfield, 1983). When it is clearly evident that the sedimentation rates have varied significantly, account must be taken of the variation in the initial ^{210}Pb concentration. In those cores with sufficient points, the first few samples were ignored for the purposes of calculating the slopes to minimise the influences of any mixing. The sedimentation rates were then used to calculate the mean flux as shown in Table 7.6.

Table 7.6: Accumulation rates calculated on the regression of the lead activity with depth. Two rates are given for each core, except for the cores from 624 m which were not deep enough. The sedimentation rate is calculated using the regression gradient, so that sedimentation rate = gradient × (ln(2)/22.26). The first rate is for the entire core and the second rate, given in the row below, is calculated minus the first sample, or in the case of the high resolution core, minus the first three samples. The average ^{210}Pb flux is calculated by multiplying the unsupported lead for each depth sample by the bulk density and the volume of the sample. The resulting value is then averaged over the number of depths sampled and multiplied by ln(2)/22.26.

Core	Gradient	Sedimentation rate (g cm^{-2} y^{-1})	Average ^{210}Pb flux (Bq m^{-2} y^{-1})
707 - rep 1	4.00	0.12	329
- first sample	3.86	0.12	145
707 - rep 2	7.57	0.23	451
- first sample	7.16	0.21	290
648 - rep 1	5.22	0.16	198
- first sample	4.82	0.14	104
648 - rep 2	4.47	0.13	295
- first sample	3.87	0.12	265
624 - rep 1	2.57	0.08	266
624 - rep 2	3.90	0.12	158
High res. core	3.41	0.10	270
- first three samples	2.42	0.07	213

7.4.6 ^{210}Pb chronologies

In Figure 7.3 d and f there is a near vertical section at the top of the cores, which indicates the effects of physical or biological mixing. Chronologies were derived from the sedimentation rates by dividing the cumulative weight (g cm^{-2}) by the sedimentation rate (g cm^{-2} y^{-1}). Chronologies are given in Tables 7.7 and 7.8, based on the whole core and where there are sufficient samples, ignoring the surface sample.

Table 7.7: ^{210}Pb chronologies for the six cores from Creag Fhiaclach. Estimated dates in years are given for all cores, based on a calculation including the uppermost sample and for the two cores from 707 m and 648 m, excluding the uppermost sample.

Depth (cm)	707 m (1)		707 m (2)		648 m (1)		648 m (2)		624 m (1)	624 m (2)
-1.5	4	-	5	-	3	-	4	-	7	4
-4.5	20	21	15	16	14	16	14	17	33	18
-7.5	48	51	28	30	28	31	28	33	102	39
-10.5	69	73	42	45	55	61	45	53		
-13.5			55	60			68	81		
-16.5			64	69			121	143		

Table 7.8: ^{210}Pb chronologies for the high resolution core from Creag Fhiaclach. Column two gives the estimated age of the peat sample based on cumulative weight including all samples. Column three gives the estimated age based on cumulative weights without the three uppermost samples.

Depth (cm)	Years	Years
-0.25	0.57	
-0.75	1.75	
-1.25	2.96	
-2.25	5.00	7.03
-2.75	8.25	11.61
-3.25	9.88	13.91
-3.75	11.66	16.41
-4.25	13.83	19.47
-4.75	15.85	22.31
-5.25	19.11	26.89
-5.75	22.13	31.14
-6.25	23.85	33.56
-6.75	25.62	36.05
-7.25	28.02	39.42
-7.75	29.62	41.68
-8.25	31.37	44.14
-8.75	33.53	47.18
-9.25	35.77	50.33
-9.75	38.05	53.54
-10.25	40.78	57.39
-10.75	43.59	61.33
-11.25	49.45	69.57
-11.75	57.19	80.47

7.4.7 Discussion

The shapes of the accumulation curves in Figures 7.3 and 7.4 cores suggests that dating using ^{210}Pb has been successful in the peat cores from Creag Fhiaclach. However, the ^{210}Pb concentration is supported in the lower layers of the peat as can be seen from the increase in ^{210}Pb at -11.75 cm in Table 7.5. Table 7.4 also shows that towards the bottom of the peat, the concentration of ^{226}Ra increases. This is because either the inorganic component in the peat increases towards the bottom or because of lateral movement of ^{210}Pb through saturated peat. Some evidence for increasing inorganic matter comes from the X-radiographs of the cores, Figures, 7.2 a-d, which show some bands of mineral material and an increase in the mineral component with depth. The thinness of the peat at Creag Fhiaclach combined with the angle of the slope and the gravel layer at the bottom of the deposit, means that although there are high precipitation inputs, the peat is relatively free draining. Therefore, unsupported lead caused by lateral movement of ^{210}Pb is an unlikely explanation.

Mean ^{210}Pb fluxes of 104-290 Bq m^{-2} y^{-1} are generally higher than the range determined by Sugden (1993) of 71.3-150 Bq m^{-2} y^{-1} for sites across Scotland. Fluxes at Creag Fhiaclach are also higher than the fluxes of 122 Bq m^{-2} y^{-1} for the Round Loch of Glenhead, Galloway and Loch Chon, in the Trossachs (Appleby *et al.*, 1990). Fluxes at Creag Fhiaclach also show an altitudinal trend to higher fluxes above the treeline. The two cores within the *Pinus* forest had average fluxes of 108-190 Bq m^{-2} y^{-1}. The lowest flux, 104 Bq m^{-2} y^{-1}, was recorded at the treeline, but the other core and the high resolution core had much higher values, 213 and 266 Bq m^{-2} y^{-1}, respectively. The treeline is not a straight line and the first replicate core from the treeline was taken from under a canopy. The other two cores were taken from more exposed stretches of the treeline. Therefore, the first replicate may represent a more forest core. A mean within-forest flux of 134 Bq m^{-2} y^{-1} is comparable with the annual flux from Loch Cionascraig in the north east of Scotland of 148 Bq m^{-2} y^{-1}(Appleby *et al.*, 1990). The fluxes from the open moorland above the treeline had averages of 145 and 290 Bq $m^{-2}y^{-1}$, though the surface flux in the second core was very high 414 Bq m^{-2} y^{-1}. Even at a more modest estimate of 290 Bq m^{-2} y^{-1} this flux is one of the highest recorded in Britain.

Sugden (1993) found considerable geographic variation in the distribution of ^{210}Pb fluxes in Scotland. This pattern coincided with the increasing precipitation from west to east, with North Uist having the highest flux, 150 ± 17 Bq m^{-2} y^{-1}. Precipitation also tends to increase with altitude. In addition, Grace *et al.* (1989) noted that the cloud line at Creag Fhiaclach tended to be at the same altitude as the treeline. This would give opportunities for increased ^{210}Pb deposition from cloud water. More recent work by Pomeroy *et al.* (1993) has shown that the distribution of snow, which is a pollutant scavenger, can affect the distribution of heavy metals. Snow tends to accumulate in the area above the treeline where conditions are more sheltered and could also be a contributor to the variation in annual fluxes.

Variation in the accumulation rates of peat at Creag Fhiaclach, 700-2300 g m^{-2} y^{-1}, is considerable and accumulation rates at Creag Fhiaclach as determined using the ^{210}Pb method are substantially higher than other rates for peat deposits in Scotland estimated using the same methodology at 95-134 g m^{-2} y^{-1} (Sugden, 1993).

Distribution of ^{137}Cs can potentially provide collaborative evidence for ^{210}Pb based chronologies. All the cores from Creag Fhiaclach have very similar ^{137}Cs profiles, Table 7.4. Concentrations of ^{137}Cs are very high in the top peat layer, but rapidly decline with depth. The chemistry of ^{137}Cs in biological systems is very similar to potassium, hence

there is downward movement through roots. The distribution of ^{137}Cs within the high resolution core shows that the decline in ^{137}Cs occurs within the first cm of the deposit.

7.5 Discussion

There is an obvious disparity in the results of the ^{14}C and ^{210}Pb dating of the peat deposit at Creag Fhiaclach (see Table 7.9). Part of this disparity will reflect the real variation in the age of the peat deposit, however the remainder can be accounted for by three hypotheses. The evidence for and against these shall be considered in turn. The simplest hypothesis is that the radiocarbon ages are a gross over-estimation of the age of the deposit. A lack of independent evidence of the rate of peat accumulation on the site makes this hypothesis difficult to refute. However, the oldest recorded tree on Creag Fhiaclach occurs at the treeline and has been there for 430 yr. (Grace & Norton, 1990), implying that the radiocarbon dates are unlikely to be over-estimates.

Previous estimates of peat accumulation rates support this argument. Peat accumulation rates in the Cairngorms between 610 m and 793 m have been estimated at 0.024 cm yr^{-1} (Pears, 1975b) this is based on a radiocarbon date of 1000 yr. at 23.5 cm (Pears, 1967). Peat accumulation rates as determined in this study from the ^{210}Pb concentrations were considerably higher than those previosly estimated by Sugden (1993) for other Scottish sites. This suggests that the ^{210}Pb is substantially under estimating the age of the peat deposits.

Under-estimation of age using ^{210}Pb forms the second hypothesis. The mechanisum for this under-estimation can be through lateral movement of ^{210}Pb caused by variations in oxidation and reduction conditions.

The final and most likely interpretation is that of a mixing profile where the rate of mixing declines with depth in a diffusion model. This hypothesis could be tested by determining the stable $^{206}Pb/^{207}Pb$ ratios (Sugden, 1993). If the ratio was constant down the profile then a mixing hypothesis would be favoured. This model would not necessarily invalidate the integrity of the stratigraphy and the palynological investigation, as mixing reduces considerably with depth. This hypothesis could be tested by simple box modelling (MacKenzie, 1982) or by looking at the distribution of pollen grains down the core. While the distribution of *Pinus* and *Calluna* is too altitude dependent the distribution of other pollen taxa may elucidate the appropriateness of this hypothesis.

Table 7.9: comparison of the ^{14}C and ^{210}Pb dates for the Creag Fhiaclach peat deposit. The ^{14}C dates from Figure 7.1 are shown collectively in column 2. The ^{210}Pb dates in columns 3, 4 and 7 are from Table 7.7. Where possible the dates are averages of the two samples, minus the top samples. Column 5 gives the chronology calculated from the high resolution core (Table 7.8), again minus the three top samples.

	^{14}C	^{210}Pb			
Depth (cm)	648 m	624 m	648 m	HR-648 m	707 m
-1.50		6			
-2.25				7	
-2.75				12	
-3.25				14	
-3.75	*			16	
-4.25				19	
-4.50		26	17		19
-4.75				22	
-5.25				27	
-5.75	*			31	
-6.25	290-0			34	
-6.75				36	
-7.25	290-0			40	
-7.50		71	32		41
-7.75				42	
-8.25	423-0			44	
-8.75	*			47	
-9.25				50	
-9.75	520-300			54	
-10.25				57	
-10.50			57		59
-10.75				61	
-11.25	700-550			70	
-11.75	290-0			80	
-13.50			81		60
-15.25	1227-940				
-16.50			143		69

7.6 Conclusions.

The disparity between the estimates of age using ^{14}C and ^{210}Pb necessitates further work to determine ages with confidence. However, both the ^{14}C and ^{210}Pb results suggest that the peat deposits at Creag Fhiaclach are in a chronological order.

8

Discussion

8.1 The relationship between the present treeline and modern pollen deposition

Pollen assemblages, both modern and sub-fossil, consist of pollen taxa derived from different source areas. Identifying the source of pollen is a critical element in interpreting sub-fossil spectra (Oldfield, 1970). Small scale spatial variations in taxa with well dispersed pollen, such as *Pinus*, are difficult to estimate (Jackson & Wong 1994) and Bennett (1995) has suggested that over-representation of *Pinus* can cause problems in determining the local extent of *Pinus* stands. More specifically, Birks (1996) has stated that a palynological approach to the question of detecting former treeline limits in the Cairngorms may be difficult because of complications from long-distance pollen transport in the region. Current models of pollen representation are limited in their application in montane regions as pollen transport mechanisms at high altitudes are poorly understood. Prentice (1985) questioned the use of the smokestack form of Sutton's equation in lowland forested landscapes on the basis that adding an elevation term reduced the relationship to basin size to unrealistic levels. Given the very regional nature of *Pinus* pollen at the treeline at Creag Fhiaclach estimations of pollen source areas using the smokestack form of the equation rather than the zero height form may be more appropriate in interpreting sub-fossil pollen assemblages. One of the most important conclusions of this thesis was that treelines can be detected at a suitably small spatial scale by exploiting the differential source areas of *Pinus* and *Calluna*. Indeed, the small spatial scale of the study was essential to ensure that the *Calluna* peak at the treeline was found.

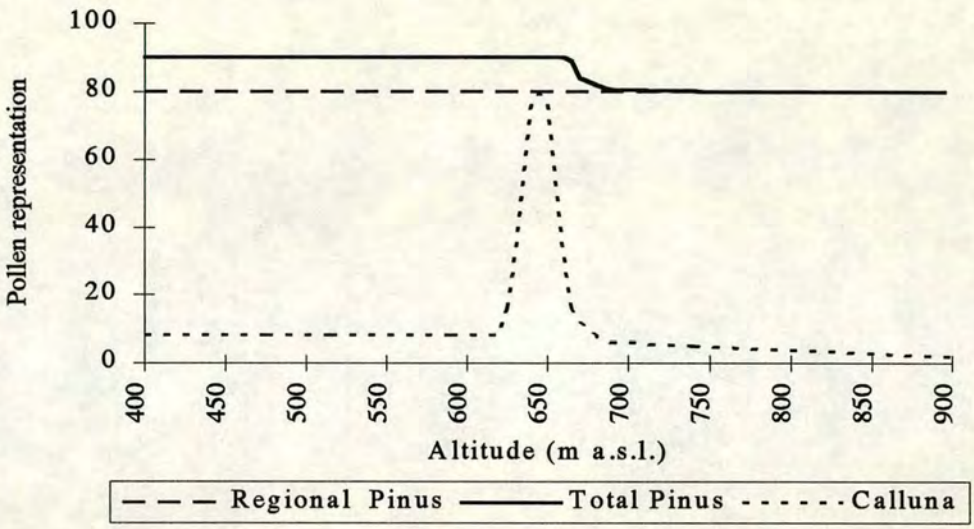
Each of the modern pollen assemblages was a combination of pollen taxa from different spatial scales. The mechanisms of pollen dispersal or the relative importance of local, extra local and regional source areas in supplying pollen to upland sites in the British Isles have not been well studied. Established models in the literature (Chapter 1) have *Pinus* pollen decreasing exponentially with distance from the forest edge. These models make

the assumption that the variation in arboreal pollen was largely a local phenomenon with little background influence from regional pollen. At Creag Fhiaclach the influence of *Pinus* pollen was primarily at the regional scale with a small contribution from the immediate stand in assemblages from under the forest canopy (Chapter 4). Deposition of locally deposited *Calluna* pollen dominated the assemblages at the treeline where flowering of *Calluna* was abundant. Most of the *Calluna* pollen in moss polsters at the treeline came from within a 1 m radius as was evident from the impact of *Juniperus communis* canopies on the attenuation of *Calluna* pollen. It is therefore factors of local *Calluna* production and dispersal that enabled the treeline to be detected using pollen quotients at this site. This is in contrast to Andersen (1970) and Bradshaw (1981) where the arboreal pollen influx itself changed over very small spatial scales. However, the landscapes in which these studies were conducted had low forest cover and the arboreal component of the regional pollen signal was correspondingly low.

The relationship between wind and vegetation structure also has implications for the detection of treelines in palynological data. Maher (1963) found a log-linear relationship between the *Picea/Pinus* ratio and altitude both above and below the *Picea* treeline in Colorado. As both of these species were trees their canopy component (*sensu* Tauber, 1965) would be subject to similar agitation through close boundary layer coupling at the canopy - atmosphere interface. Below the *Picea* treeline, trunk space movement of *Pinus* pollen gradually declines with altitude so the highest *Picea/Pinus* ratio is reached at the treeline. Mahers' (1963) approach cannot be applied at Creag Fhiaclach because of the different stature of *Pinus* and *Calluna* at the treeline. Below the treeline there was no significant variation in the *Pinus/Calluna* pollen quotient with altitude. The dramatic difference in stature between *Pinus* and *Calluna* dominated vegetation at the treeline has two implications for the pollen quotients. Firstly, the more turbulent atmosphere experienced by the taller *Pinus* canopies will mean a substantial proportion of the pollen produced by the canopy contributing to the canopy component rather than trunk space pollen component. Secondly, the *Pinus* stand provides a sheltered environment for *Calluna* in the immediate vicinity of the treeline. Not only was *Calluna* more productive in this environment, but the reduced wind speeds would mean that most pollen transport would be under the canopy and source areas will therefore be very small. Thus, the relative proportions of the pollen taxa contributing to the pollen assemblages may be as

demonstrated in Figure 8.1. Local pollen deposition was classically considered to be very important within forests (Andersen, 1970; Bradshaw, 1981) and here it has been shown to be important within heath vegetation.

Figure 8.1: Hypothetical model of *Pinus* and *Calluna* pollen deposition at the Creag Fhiaclach treeline. *Calluna* pollen has low representation in the forest because of shade from the canopy. At the treeline *Calluna* flowers heavily in the shelter created by the forest stand. Most of this pollen is deposited locally as wind speeds are relatively low. With increasing distance from the treeline, *Calluna* pollen representation drops rapidly with increasing altitude as the influence of the shelter is reduced. At higher altitudes *Calluna* is much more closely coupled to wind speeds and pollen production drops and deposition will be over wider areas. In contrast, *Pinus* pollen representation in this turbulent environment is mostly regional with a small contribution to the pollen assemblages from the immediate stand.



Previous treeline determinations on the basis of AP/NAP or selected pollen taxa need to be carefully interpreted in terms of the regional pollen signal. The very different pollen distribution of *Pinus* and *Calluna* at the treeline at Creag Fhiaclach enable the position of the treeline to be detected from a simple pollen quotient. However, quotients have a limitation in that high quotients can be derived from forest, *Juniperus communis* stands or high altitude heath. Discriminant function analysis can be used to distinguish between forest and high altitude heath assemblages on the basis of minor taxa analogous to the indicator species approach of Spear (1989). However, some discrepancies occurred with the discriminant function analysis, probably caused by the low counts for the minor taxa.

As the quotients produced similar results to the discriminant analysis, the extra counting required to alleviate discrepancies in the discriminant analysis is unjustified.

Interpretation of palynological data for previous treeline fluctuations must consider the dispersal of the two main contributors to pollen assemblages at the treeline. A change in altitude of the treeline of as little as 25 m (Figure 4.2) should be detectable at Creag Fhiaclach. As this approach to changes in detecting the treeline is so sensitive, in periods of rapid treeline fluctuations there is a possibility that low temporal resolution can obscure fluctuations. Therefore, this system is only of use in a sampling regime were fine temporal resolution is employed. Variation in the modern pollen assemblages also indicates the need for replicated samples.

In addition there are still several inherent assumptions in the interpretation of sub-fossil pollen data, the influences of which are difficult to assess. One of the main assumptions is that the abundance of *Calluna* and *Pinus* in the past shows the same pattern as present. This is particularly pertinent if there had been fires on the site in the past. Intensity of fire will have different effects on the productivity of these two species as *Pinus* is much more resilient to fire than *Calluna*. In the Boreal zone *Pinus* forests naturally regenerate themselves only after major disturbance, primarily caused by fire. Infrequency of disturbance may thus also explain the stability of the treeline. Regional *Pinus* pollen may also be influenced by deforestation and planting over a wide spatial scale.

8.1.1 Implications for the interpretation of *Pinus* history in Scotland

One of the key questions in the interpretation of pollen data is the quantity of pollen necessary from an individual taxon to indicate local presence of that species. As *Pinus* played such a major role in the Holocene vegetation history of the British Isles (Godwin, 1975; Bennett, 1984) the quantity of *Pinus* pollen required to indicate local presence has often been considered in the literature. *Pinus* is a copious pollen producer and is generally considered to be over-represented in forest stands (Andersen, 1970; Bradshaw, 1981). *Pinus* is also wind pollinated and very commonly shows long distance transport (Tyldesley, 1973; Prentice, 1978; Huntley & Birks, 1983; Bennett, 1984; MacDonald & Ritchie, 1986; Schwartz, 1989), thus, *Pinus* pollen may be found in sediments at localities where trees were never present.

Faegri & Iverson (1975), Bennett (1983) and Birks (1977) have suggested that to attain accurate estimates of the relative importance of different taxa in the pollen rain all land pollen taxa should be included in the sum. Commonly, 20% *Pinus* pollen expressed either in terms of TLP or of tree and shrub pollen has been taken to indicate local presence of *Pinus* (Bennett, 1984; Huntley & Birks, 1983). However, some marked variation from 20% has been shown in other studies. Ward *et al.* (1987), in a modern pollen rain study at Rannoch Moor found that at one point the representation of *Pinus* in the modern pollen was as low as 1% within 100 m of a stand of trees. Similarly, recent work by Fossitt (1994) in lake sediments from Donegal using the presence of stomatal guard cells and *Pinus* pollen frequencies demonstrated the local presence of *Pinus* where the *Pinus* pollen frequencies were as low as 5%. In light of this a recent account of the history of *Pinus* in Scotland (Bennett, 1995) was based on 5% *Pinus* pollen rather than the more traditional threshold of 20%. Presence of stomatal guard cells are thought to indicate the distribution of *Pinus* more accurately than pollen because needles are less likely to be found distant from their source than pollen (Birks & Birks, 1980; Bennett, 1984). However, the presence of needles on the surface of the Ciste Mhearad snow bed demonstrates that small numbers of needles are capable of being widely distributed in this environment.

From the stomatal study used to indicate local presence of *Pinus* by Fossitt (1994) long distance transport was inferred to contribute comparatively small quantities of pollen. As outlined above this frequency has been between 5% and 20% for the British Isles. The present study has shown that even over a small spatial extent there can be large variation in the proportional representation of *Pinus* in close proximity to a stand of trees. Figure 4.3 showed that the lowest quotient in the modern pollen rain samples was 14% P*100/(P+C) at 758 m. As the other taxa were minor components, all the modern quotients from Creag Fhiaclach fall well above the minimum 5% P/TLP level for indicating local presence. However, the very high representation of *Pinus* at Ciste Mhearad has potentially worrying implications for mapping previous distributions of *Pinus* from pollen data. Clearly high altitude cores, with their high regional influence on the pollen spectrum can only be utilised in broad brush reconstructions at the landscape level. Data obtained from cores from other potential sources of regional pollen, e.g. lakes, would also need to be interpreted with caution. Ideally, reconstructions of past

populations should be on the basis of pollen that can be shown to have a high local pollen component.

The highly regional nature of the *Pinus* pollen distribution in the Cairngorm region suggests that the spread of *Pinus* into Scotland as determined by the pollen record may not be as dramatic an expansion as has previously been stated. A much less dense distribution of *Pinus*, which contributed highly to the regional pollen component could incorrectly be interpreted as representing wider distribution of the species. The probability of significant quantities of *Pinus* pollen from Scandinavia being deposited in Scotland has already been discounted by Bennett (1984), but equally *Pinus* pollen need not necessarily have come from Ireland or England as also suggested by Bennett (1984). *Pinus* pollen from small or scattered stands already established in Scotland could provide sufficient pollen for long distance transport to give an erroneous picture of the history of *Pinus* from pollen alone. This will only be true in cases where total land pollen is low or where there are few local pollen producers, e.g., early in the Holocene, in lakes, profiles from raised bogs and at high altitudes. If the argument of regionally distributed *Pinus* pollen in Scotland from Scottish sources was accepted then it follows that there are implications for interpreting the origin of *Pinus* on the basis of pollen distribution. There is still a requirement for more basic research on the taphonomy of *Pinus* pollen, particularly the role of long distance or regional pollen which has been inadequately documented so far. Perhaps studies of the genetic variation of *Pinus* populations in Scotland will assist in determining the pattern of *Pinus* colonisation and subsequent decline and hence the representation of *Pinus* pollen in a temporal and spatial framework can be extrapolated laterally. Bennett (1995) suggested that one area for future research on the history of *Pinus* in Scotland should be parallel studies in distribution of stomatal guard cells when pollen frequencies are low. In view of the results presented here parallel studies should also occur where *Pinus* frequencies are high.

8.2 Past treeline fluctuations

Based on the model of pollen deposition at the treeline there are three possible interpretations of the palynological data:

1. the treeline has declined along its entire length, but the cores at the northern end are too young to detect the change

2. the treeline has declined at the southern end only
3. the apparent decline in the treeline at the southern end is an artefact from changes in the distribution of *Juniperus communis* and the treeline is relatively stable.

The first interpretation can be revoked on the basis of the radiocarbon dates given in Chapter 7. These dates suggest that at -3.75 cm all the cores were enriched relative to modern and thus while it is difficult to determine an exact age, all the material at this depth is relatively modern. If the treeline had declined along its length in this time, there would most certainly be some evidence in the form of rotting material still present on the site. It is therefore highly unlikely that this interpretation is correct.

The second interpretation must take into account the dynamic interface between the treeline and the heath vegetation. Above the treeline only the most sheltered southern end of the ridge showed any potential evidence of a previously higher treeline. However, the other three replicates could have been of a lesser age at -3.75 cm because of more rapid peat growth. Evidence of the higher treeline may therefore have been lost at the bottom of these profiles. Figure 7.1 demonstrated that there was no significant difference in the radiocarbon ages of the five replicates at -3.75 cm. A precise date for the switch from forest to heath in replicates four and five was very difficult to determine as the radiocarbon dates at this depth were enriched relative to modern. The ^{210}Pb dating aged the -3.75 cm depth at 707 m in the 28-51 year range (Table 7.7). While this age range was concurrent with the radiocarbon dates the two methods overall were not comparable and the results have to be interpreted with caution. However, if the ^{210}Pb dates are correct this would imply that the decline in the treeline at the southern end of the site occurred within the last 50 yr. Even if this decline occurred over the last 150 yr. one would expect there still to be evidence of tree remains above the treeline or if the cause of decline was fire related there would be an obvious charcoal layer in the profiles at -3.75 cm.

The fire history at Creag Fhiaclach was difficult to determine. The highly humified nature of the peat meant that the best pollen preparations were obtained using a whirlie mixer and only infrequent small fragments of charcoal were observed. There is little evidence of fire history in the Cairngorm region. Some anecdotal evidence was given by MacMillan

(1907) that a fire started south-east of Loch-an-Eilein in 1899 caused extensive damage to vegetation which largely recovered by 1907.

The second interpretation is feasible, however a much more probable hypothesis is that the apparent decline in elevation of the treeline at the southern end of the ridge was caused by a change in the distribution of *Juniperus communis*. Sterile *Juniperus communis* canopies result in pollen assemblages which are indistinguishable from those of *Pinus* forest. Thus, the fourth and fifth replicate pollen profiles at 707 m could be interpreted as a decline in the dense band of *Juniperus communis* and not a decline in the elevation of the *Pinus* forest. Both the time scales involved and the stability of the treeline indicated in the other replicate cores support this hypothesis assuming that the modern pollen-vegetation relationship holds.

Stability of treelines over various temporal scales has been shown to occur in other locations. In the Rocky Mountains treelines can be found which have been virtually stable for the last 5000 years (Ives & Hansen-Bristow, 1983). Stability has also been shown in latitudinal treelines during the Holocene (Gajewski *et al.*, 1993; Payette *et al.*, 1989).

At Creag Fhiaclach replicate cores from within the forest had consistently high *Pinus* representation indicating that there has been virtually continuous forest cover as opposed to O'Sullivan's (1973b) findings at Abernethy where there was only evidence of discontinuous forest cover. O'Sullivan's oldest core was 1505 $\pm$ 150 BP which was comparable with the oldest radiocarbon date, 1200 BP, from Creag Fhiaclach. However, anthropic influences at the lower altitude and easier accessibility of the site at Abernethy could explain the dynamics of the forest cover. Bioturbation could also cause uniform pollen assemblages down a profile, but the radiocarbon and ^{210}Pb dating showed the chronological integrity of the profiles and indicated that these pollen assemblages were representing stable plant communities at Creag Fhiaclach.

8.3 Factors determining the position of the current treeline

If the *Pinus* treeline at Creag Fhiaclach has been stable at its present elevation since AD 723-1010, then this challenges the classic idea of treelines being coupled to climate. The stability of the treeline as inferred from the palynological study suggests that the modern

treeline is below the potential maximum elevation as determined by climate at the site. Further evidence for a suppressed treeline at Creag Fhiaclach comes from a previous study of annual ring widths by Grace & Norton (1990) who demonstrated that correlations between annual ring widths and summer and winter temperatures were stronger at lower altitudes than at the treeline and the narrowest rings occurred 150 m below the modern treeline. The highest altitude trees sampled by Grace & Norton (1990) were krummholtz trees at the treeline. The lower stature and resultant higher tissue temperatures (Wilson *et al.*, 1987; Grace *et al.* 1989) of krummholtz trees adequately explains the otherwise unexpected variation in ring widths. There is also an increase in the ratio of photosynthetic to non-photosynthetic tissues in krummholtz trees. But can the interaction between stature and climate explain the position of the present treeline or, more critically, the treeline stability?

Elevation of treelines can be explained in terms of carbon balance (Stevens & Fox, 1991). With increasing altitude both temperature and hence rate of photosynthesis decline to a point where carbon fixation is insufficient to maintain life. However, the carbon balance of the krummholtz trees at Creag Fhiaclach is far from critical from the annual ring width evidence. This narrow band of krummholtz trees may therefore represent only the lower altitudinal limit of this tree form and not its climatically determined limit.

The stability of the treeline as indicated from the palynological study and the annual ring width evidence indicates that if either summer or winter temperatures are the main determinants of treeline elevation at this site then the relationship is complex and requires further evaluation. Trees sampled by Grace & Norton (1990) ranged from 100-250 years old and the older trees, therefore, established during the Little Ice Age. A comprehensive study of the maximum late-wood density in krummholtz trees and saplings at the treeline would be instructive as maximum late-wood densities are better able to predict summer temperatures than annual ring widths (Schweingruber *et. al.*, 1979).

The idea of the current treeline in the Cairngorms being suppressed relative to the climatic potential is not new. Pears (1967) on the basis of temperature data estimated that the true altitude for the treeline in the Cairngorms would be at 760 m and that it was a combination of wind speeds and grazing that suppressed the treeline and reduced scrub

formation. However, Pears (1967) claimed that temperature had a role in seedling establishment as evidenced by an increase in seedling establishment between the warmer summers of 1954-1959 and reduction in the harsh winter of 1963-1964 at Creagan Leth-Choin. Kullman (1985) also demonstrated that establishment of *Pinus* seedlings was positively correlated with mean June-September air temperatures in Central Sweden. However, an increase in the altitudinal limit of *Pinus* caused by trees which established in the 1950s also in Central Sweden (Kullman, 1993) is probably not correlated with temperature as Jones *et al.*, (1986) showed climate to be relatively stable over this period. Kullman (1993) suggested on this basis that treelines can advance slowly upslope during periods of climatic stability. This is in contrast with Hättenschwiler & Körner (1995) who found that temperature increase over 1982-1991 did not stimulate upslope migration in populations of *Pinus* in the Swiss Alps.

The migration response to climate change can also be impeded by successional processes and species interactions. Responses of plant communities to climate change are facilitated through birth, growth and death of individuals. A change in environmental conditions shifts competitive balances and therefore affects the establishment of plants and succession (Prentice, 1986). The response time of the vegetation may be at a different temporal scale to climate variables. This has complex influences on tree populations because of niche differentiation between seedlings, saplings and canopy trees.

Spatial variability in the environment adds another layer of complexity and the treeline ecotone is one of the most environmentally heterogeneous montane zones. The functional diversity of the vegetation and the variation in relief cause a variety of microclimates with a range of conditions which already exceeds those predicted by models of climate change. This diversity of microsites confers a natural stability on treeline ecotones and climate change of a few degrees is therefore unlikely to affect the overall structure of the treeline because of this variation in microsites. The dynamic interface between the forest and heath in the palynology study indicates the stochastic nature of environment at the treeline, which could, ironically, contribute to its altitudinal stability. In considering the change in climate in relation to vegetation zones in the Alps, Ozenda (1983) points out that the average width of a vegetation zone was 700 m and the change in temperature over this range of altitude was in the order of 4 °C suggesting that vegetation is stable over this

range of temperatures. Indeed, maximum variation in treelines in the Alps from pollen records was 150-200 m during the Holocene (Bortenschlager, 1993).

Previous studies of vegetation histories in mountain regions have shown that migrational changes can rarely be explained in terms of responses to variation in temperature (Davis *et al.*, 1980; Spaulding, 1984). Other ecological factors may influence the upper limit to trees at Creag Fhiaclach. The influence of grazing at the upper treeline is an open question. At the Cairn Gorm a recent increase in the performance of *Pinus* seedlings was thought to be caused by reduction in grazing through anthropogenic disturbance (Hester & Miller, 1995). Similarly, in the valley below the *Pinus* stand at Creag Fhiaclach a reduction in red deer numbers has resulted in a flush of growth in previously suppressed saplings. However, no such flush has occurred above the upper treeline.

Climate influences on soil processes and subsequently on vegetation is an area that is undergoing substantial research at present, though most of this is concentrated in the Arctic rather than alpine regions. Soil processes, particularly soil development, is thought to cause lags in the response of vegetation in cold climates to temperature increases. Opinions on the effects of edaphic lags vary. Holtimeier (1995) outlines the processes underpinning edaphic lags in treeline dynamics. Soil processes can also vary spatially and natural soil acidification has been shown to occur at different rates in the same climate (Pennington, 1986). Soil processes may also influence distribution of plant communities indirectly through the distribution of soil organisms such as mycorhizzal fungi. Unfortunately, fungal spores were not recorded from Creag Fhiaclach so this possibility remains.

The stability of the *Pinus* treeline at Creag Fhiaclach as indicated by the palynological study suggests that the treeline is not simply determined by temperature. This is supported by the previous physiological research at this site.

8.4 Prediction of future treeline fluctuations.

Predicting elevation of the treeline at Creag Fhiaclach under future climate change scenarios is currently difficult for a number of reasons. The majority of future climate scenarios are for warmer climates. The radiocarbon dates from Creag Fhiaclach suggest

that this treeline was certainly at its current position through the Little Ice Age, but may not have been in existence during the mid-Holocene optimum. Thus, while the palynological data suggests that the treeline can remain stable through colder periods, the hypothesis that it may migrate under a prolonged period of 2 °C higher temperatures cannot be tested at Creag Fhiaclach as the peat is not of a sufficient age. Higher temperatures may dry out the thin blanket peat and the resultant water stress may prevent upslope advancement of the treeline. Higher temperatures will cause the rate of decomposition to increase and the depth of peat could be reduced to a point where it cannot support trees. Lapse rates may also change considerably under different climate conditions. The steep lapse rate in the Cairngorms is the result of a meeting of Atlantic and polar air masses and this may alter radically. A lowering of the lapse rate would result in correspondingly higher warming at higher altitudes. The role of direct CO_2 fertilisation in determining treeline elevations in a higher CO_2 environment has been questioned by Graumlich (1991). The higher CO_2 concentrations distinguish the mid-Holocene optimum from future climate warming scenarios. Increased atmospheric CO_2 may stimulate upslope advance or its effects could be limited by below ground processes.

The complex interactions of species at both altitudinal and latitudinal range boundaries need to be included in future models of climate change (Woodward, 1993). However, before this will be possible more research is required to understand why these boundaries exist and what the processes are that regulate their distribution.

8.5 Concluding remarks

1. Interpretation of palynological data from montane regions is only useful in light of modern pollen references and these should include assemblages from several spatial scales. Spatial variation in pollen percentages means that replication of both modern and sub-fossil assemblages is also important. Extreme caution is clearly needed when interpreting temporal changes in vegetation from a single core.

2. Quotients of selected taxa can be used to detect small scale treeline fluctuations though care is needed in interpreting the direction of movement. Discriminant function analysis can aid interpretation in this respect.

3. Pollen transport in montane environments is a key area for further research. Without this interpretation of high altitude pollen data will be extremely difficult and important lessons from past climatic changes may be missed. Current models of pollen representation are very limited in their application at the treeline.

4. It may be possible to formulate a new model on the data from the modern pollen rain study in conjunction with measurements of wind speed data collected during previous research at this site. Such a model should address the question of determining the local pollen source area of *Pinus* at the treeline. This study of the treeline at Creag Fhiaclach has made a contribution to the research on Holocene treeline fluctuations by providing a method by which questions such as this can be addressed.

5. The stability of the treeline at Creag Fhiaclach through the Little Ice Age suggests that the treeline is suppressed below its maximum potential altitude as determined on the basis of temperature alone. This equilibrium position of the treeline is most likely a complex interaction of microclimate heterogeneity and population demography.

6. The role of disturbance, *visa vi* fire cannot be completely ruled out as the charcoal history is incomplete.

7. Other hypotheses, both environmental and ecological as discussed above, can be evoked to explain both the elevation and stability of the treeline. These questions also need addressing to aid with future management of the treeline and will be central to any initiatives to re-establish treelines or sub-alpine scrub in Scotland.

8.6 Future research

The whole issue of scale in relation to *Pinus* and *Calluna* pollen deposition underlies this thesis. Acquisition of more absolute data on *Pinus* influx from local and regional sources could be combined with wind speed data in a fluid dynamics model to produce a more widely applicable model of pollen distribution at treelines.

Two components of the palynological data were not fully utilised in this study and could form the basis of further research. Firstly, the geometrical nature of the sampling could

provide more information on spatial processes. Kriging was considered as a possible avenue to explore the spatial auto-correlations, but unfortunately could not be used because of insufficient points (Webster, 1985). Secondly, the distribution of rhizopods which were highlighted in the PCA and RDA deserve more attention. Very little is known of the ecology of these protozoa, but their hydrological response curves could be used to test Dubois & Ferguson's (1985; 1988) hypothesis that *Pinus* cannot establish on wet surfaces. In addition, dating in such shallow deposits was difficult and the conflict between the radiocarbon and ^{210}Pb dating needs to be resolved. In conjunction with resolution of the dating, the initiation of peat on this site could be explored further. Iniation of peat formation in the Cairngorm region is generally dated much earlier (8000 - 4000 BP) than has been found at Creag Fhiaclach (Birks, 1975; Pears, 1975a and Dubois & Ferguson, 1985). The peat iniation at Creag Fhiaclach could have genuinely been very late, or the peat samples from the site could contain modern material (the deposit is shallow), or original peat could have been removed by fire.

On a wider spatial scale, the static nature of the *Pinus* treeline at Creag Fhiaclach gives no indication of the extent of former tree cover in the Cairngorms as a whole. The use of quotients to detect forest cover at higher altitudes in the Cairngorms is most likely to be profitable at sites were there was some macrofossil evidence of previous trees. Pears (1967) has suggested a broad scrub zone occurred above the highest treeline in the sub-boreal. If this scrub zone had a sizeable *Juniperus communis* component this may not be detectable from the use of quotients. On much wider geographical scales quotients could be used effectively at any treeline or vegetation boundary where there are two strong pollen producers associated with juxtaposing vegetation types. The most obvious place to apply the approach outlined in this thesis would be at the *Pinus* treelines of northern Norway which are relatively undisturbed.

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Appendix I: Vegetation Synoptic Tables.

Synoptic tables of vegetation composition along the altitudinal gradient at Creag Fhiaclach. Frequency refers to occurrence in five quadrats. Quadrats were 10 m x 10 m to 648 m and 4 m x 4 m at altitudes above this. Mean is the mean percentage cover across the five quadrats.

606 m

Species	Frequency	Mean
Pinus sylvestris	V	46
Vaccinium myrtillus	V	37
Hylocomium splendens	V	32.4
Vaccinium vitis-idaea	V	22
Rhytidiadelphus squarrosus	V	15.4
Pleurozium schreberi	V	6
Deschampsia flexuosa	V	5.8
Calluna vulgaris	IV	11
Hypnum cupressiforme	IV	6
Campanula rotundifolia	IV	0.8
Hypogymnia physodes	IV	0.8
Empetrum nigrum	III	5.2
Dicranum fuscescens	II	4.4
Erica cinerea	II	0.4
Odontoschisma sphagni	II	0.4
Plagiothecium undulatum	II	0.4
Pseudoscleropodium purum	I	1
Ptilium crista-castrensis	I	0.4
Sphagnum cuspidatum	I	0.4
Cladonia digitata	I	0.2
Cladonia polydactyla	I	0.2
Mnium hornum	I	0.2
Plagiochila spinosa	I	0.2

624 m

Species	Frequency	Mean
Pinus sylvestris	V	88
Hylocomium splendens	V	46
Vaccinium myrtillus	V	34.8
Vaccinium vitis-idaea	V	31
Deschampsia flexuosa	V	14.8
Calluna vulgaris	IV	7.6
Dicranum fuscescens	III	6
Empetrum nigrum	III	5.4
Rhytidiadelphus squarrosus	III	3.4
Pleurozium schreberi	III	3.2
Hypnum cupressiforme	III	1
Campanula rotundifolia	III	0.6
Hypogymnia physodes	II	1.8
Ptilium crista-castrensis	II	0.6
Erica cinerea	II	0.4
Cladonia carneola	I	0.2
Cladonia polydactyla	I	0.2
Cladonia pyxidata	I	0.2
Juniperus communis	I	0.2
Odontoschisma sphagni	I	0.2
Potentilla erecta	I	0.2
Pseudoscleropodium purum	I	0.2

636 m

Species	Frequency	Mean
Pinus sylvestris	V	62
Hylocomium splendens	V	29
Deschampsia flexuosa	V	26.4
Vaccinium myrtillus	V	19.2
Vaccinium vitis-idaea	V	17.2
Calluna vulgaris	IV	16
Rhytidiadelphus squarrosus	IV	2.6
Potentilla erecta	IV	2.2
Juniperus communis	III	5.2
Pleurozium schreberi	III	2.6
Empetrum nigrum	III	2.4
Galium saxatile	III	1.8
Erica cinerea	III	0.8
Hypogymnia physodes	III	0.6
Dicranum fuscescens	II	4.4
Viola canina	II	1.2
Hypnum cupressiforme	II	0.6
Campanula rotundifolia	II	0.4
Luzula campestris	II	0.4
Odontoschisma sphagni	II	0.4
Ptilium crista-castrensis	II	0.4
Salix lapponum	II	0.4
Carex echinata	I	3
Cladonia ramulosa	I	3
Juncus trifidus	I	2
Festuca ovina	I	1
Sphagnum palustre	I	1
Agrostis capillaris	I	0.2
Carex demissa	I	0.2
Cladonia chlorophaea	I	0.2
Cladonia macilenta	I	0.2
Euphrasia officinalis agg.	I	0.2
Lycopodium clavatum	I	0.2
Mnium hornum	I	0.2
Myosotis discolor	I	0.2
Pinguicula vulgaris	I	0.2
Polygala vulgaris	I	0.2
Polytrichum juniperinum	I	0.2
Pseudoevernia furfuracea	I	0.2
Pseudoscleropodium purum	I	0.2
Succisa pratensis	I	0.2
Taraxacum officinalis agg.	I	0.2

648 m

Species	Frequency	Mean
Calluna vulgaris	V	60
Hylocomium splendens	V	46
Vaccinium myrtillus	V	27.4
Rhytidiadelphus squarrosus	V	7.8
Deschampsia flexuosa	V	7.4
Vaccinium vitis-idaea	V	3.2
Erica cinerea	IV	1.8
Juniperus communis	III	11
Pseudoscleropodium purum	III	9
Galium saxatile	III	0.8
Potentilla erecta	III	0.6
Pinus sylvestris	II	29
Empetrum nigrum	II	2.4
Plagiothecium undulatum	II	0.4
Ptilium crista-castrensis	II	0.4
Cladonia portentosa	I	0.4
Cladonia chlorophaea	I	0.2
Cladonia squamosa	I	0.2
Hypnum cupressiforme	I	0.2
Hypogymnia physodes	I	0.2
Odontoschisma sphagni	I	0.2
Plagiochila spinosa	I	0.2
Primula vulgaris	I	0.2

677 m

Species	Frequency	Mean
Calluna vulgaris	V	73
Hylocomium splendens	V	29
Deschampsia flexuosa	V	12
Erica cinerea	V	8
Vaccinium myrtillus	IV	2.8
Cladonia cilliata	IV	1.8
Rhytidiadelphus squarrosus	IV	0.8
Vaccinium vitis-idaea	III	4.2
Juniperus communis	III	3.6
Trichophorum cespitosum	III	2.6
Potentilla erecta	III	1.4
Cladonia portentosa	III	0.9
Juncus trifidus	II	1.2
Hypnum cupressiforme	II	0.6
Viola canina	II	0.6
Cladonia chlorophaea	II	0.4
Pseudoscleropodium purum	II	0.4
Succisa pratensis	I	1
Carex binervis	I	0.2
Cladonia furcata	I	0.2
Cladonia squamosa	I	0.2
Cladonia uncialis ssp. *biuncialis*	I	0.2
Dicranum scoparium	I	0.2
Empetrum nigrum	I	0.2
Euphrasia officinalis agg.	I	0.2
Hypericum pulchrum	I	0.2
Plagiochila spinosa	I	0.2
Plagiothecium undulatum	I	0.2
Pleurozium schreberi	I	0.2
Polygala vulgaris	I	0.2
Taraxacum officinalis agg.	I	0.2

707 m

Species	Frequency	Mean
Calluna vulgaris	V	62
Cladonia portentosa	V	16
Erica cinerea	V	14
Hylocomium splendens	V	11
Vaccinium myrtillus	V	6.6
Deschampsia flexuosa	V	3.8
Rhytidiadelphus squarrosus	V	1.4
Vaccinium vitis-idaea	IV	10.6
Trichophorum cespitosum	IV	1.4
Cladonia cilliata	III	4.4
Campanula rotundifolia	III	0.8
Potentilla erecta	III	0.6
Pinus sylvestris	II	3.4
Cladonia furcata	II	0.6
Hypnum cupressiforme	II	0.6
Hypogymnia physodes	II	0.4
Juniperus communis	I	2
Empetrum nigrum	I	1
Carex binervis	I	0.2
Cladonia chlorophaea	I	0.2
Cladonia gracilis	I	0.2
Cladonia rangiferina	I	0.2
Cladonia subcervicornis	I	0.2
Cladonia uncialis ssp. *biuncialis*	I	0.2
Dicranum scoparium	I	0.2
Genista anglia	I	0.2
Polytrichum juniperinum	I	0.2
Ptilium crista-castrensis	I	0.2

717 m

Species	Frequency	Mean
Calluna vulgaris	V	66
Hylocomium splendens	V	17
Vaccinium vitis-idaea	V	14.8
Erica cinerea	V	12
Deschampsia flexuosa	V	7.8
Potentilla erecta	V	2.2
Trichophorum cespitosum	III	2.2
Hypogymnia physodes	III	0.6
Rhytidiadelphus squarrosus	III	0.6
Cladonia cilliata	II	3.2
Carex binervis	II	1.4
Vaccinium myrtillus	II	0.6
Cladonia polydactyla	II	0.4
Cladonia squamosa	II	0.4
Cladonia uncialis ssp. *biuncialis*	II	0.4
Hypnum cupressiforme	II	0.4
Juniperus communis	I	2
Cladonia rangiferina	I	0.6
Empetrum nigrum	I	0.4
Succisa pratensis	I	0.4
Blechnum spicant	I	0.2
Campanula rotundifolia	I	0.2
Cladonia bellidiflora	I	0.2
Cladonia carneola	I	0.2
Cladonia chlorophaea	I	0.2
Cladonia coccifera	I	0.2
Cladonia furcata	I	0.2
Cladonia glauca	I	0.2
Cladonia portentosa	I	0.2
Dicranum scoparium	I	0.2
Polytrichum juniperinum	I	0.2
Racomitrium lanuginosum	I	0.2
Viola canina	I	0.2

758 m

Species	Frequency	Mean
Calluna vulgaris	V	59
Erica cinerea	V	10.2
Trichophorum cespitosum	V	10
Hylocomium splendens	V	2.8
Vaccinium vitis-idaea	IV	15.4
Cladonia portentosa	IV	13
Hypnum cupressiforme	IV	3
Deschampsia flexuosa	IV	1
Cladonia coccifera	III	0.8
Empetrum nigrum	II	2.2
Juncus trifidus	II	2
Cladonia portentosa	I	2
Carex binervis	I	0.2
Carex hostiana	I	0.2
Cladonia digitata	I	0.2
Cladonia uncialis ssp. *biuncialis*	I	0.2
Dactylorhiza maculata	I	0.2
Dicranum scoparium	I	0.2
Lycopodium clavatum	I	0.2
Pseudevernia furfuracea	I	0.2
Sphagnum palustre	I	0.2
Vaccinium myrtillus	I	0.2

Appendix II: Description of Rhizopod palynomorphs from Creag Fhiaclach.

Rhizopod tests that are formed mainly from organic secretions are referred to as agglutinate and are of two types, those which construct daughter tests from quartz and diatoms (mostly species of Difflugiidae) and those which ingest other testate species, e.g., *Nebela* spp. and *Heleopera* spp. (Ogden & Hedley, 1980). Predatory rhizopods use the shell plates and the reserve plates that are stored in the cytoplasm of their prey for daughter cell formation. *N. collaris* shell plates obtained by ingestion are found throughout the cytoplasm and, in culture, *N. collaris* produces daughter cells that are atestate (MacKinlay, 1936). Rhizopod species which form plates are separated into three types dependent on the nature of the plates (Ogden & Hedley, 1980). Species constructing plates from protein are subdivided into two types, those composed of homogeneous protein and those composed of numerous alveoli plates. Superfamily Euglyphacea and some species from *Difflugia*, *Lesquereusia* and *Quadrullela* genera create their own siliceous shells. Finally, *Paraquadrulla irregularis* and *Cryptodifflugia ouiformis* produce plates that are calcareous.

The following four taxa were recognised in the peat extracts from Creag Fhiaclach:

(i) Clear textured
These laterally flattened tests were colourless and composed of overlapping rhomboid plates with rounded corners arranged in a regular pattern. This morph keyed out as *Euglypha rotunda* Wiles in Corbert (1973) distinguished by the absence of spines and a circular aperture with no thickening. Absence of thickening around the aperture is important for distinguishing *Euglypha rotunda* from spineless forms of *Euglypha stigosa* (Corbet, 1973).

(ii) Clear smoother
Specimens of this morph were also colourless and had tiny irregular geometrically shaped plates Figure II.1). There was very obvious thickening around the aperture and the test was laterally flattened. Lateral pores could be distinguished at x 600 magnification; these were towards the aperture. In the key to genera (Corbet, 1973) this morph keyed out as *Nebela*. Getting an identification at species level in Corbet (1973), was difficult but, the morph was most similar to *Nebela collaris* in Ogden & Hedley (1980). There are some discrepancies in the descriptions of the species from Corbet (1973) and Ogden & Hedley (1980). Corbet (1973) states that *Nebela collaris* Ehrenberg is yellow and has no lateral pores, while Ogden & Hedley (1980) describe the test of *Nebela collaris* Ehrenberg as being colourless and having lateral pores. It was decided that this morph most closely resembled the description of *Nebela collaris* Ehrenberg from Ogden & Hedley (1980) and was referred to as such in this thesis.

(iii) Brown hatch
Colour of tests varied from pale to a definite brown. Tests were ovoid, flattened and composed of ovoid imbricated plates. Apertures were oval and surrounded by plates. This morph keyed out as *Assulina muscorum* Greef in Corbet (1973). A band of organic cement around the aperture that should be a feature of this species (Cash & Hopkinson, 1905; Corbet, 1973; Ogden & Hedley, 1980) was not immediately apparent in the specimens observed from Creag Fhiaclach (Figure II.2). The process of pollen preparation may have damaged this. Fresh specimens would need to be compared to the

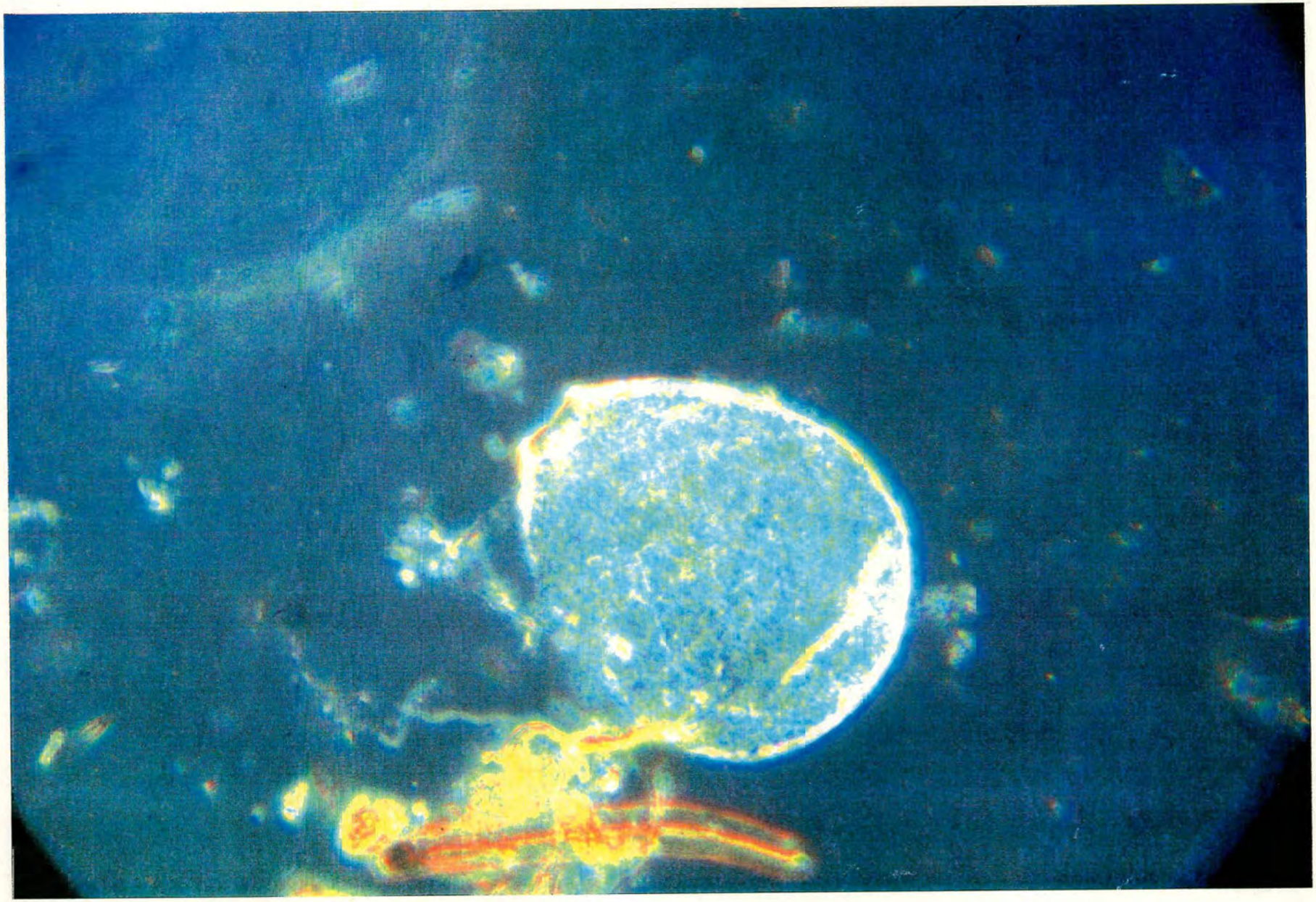

Figure II.1: c.f. *Nebela collaris* Ehrenberg, using dark field photography at × 1000 under oil immersion on a Leitz Ortholux 2.

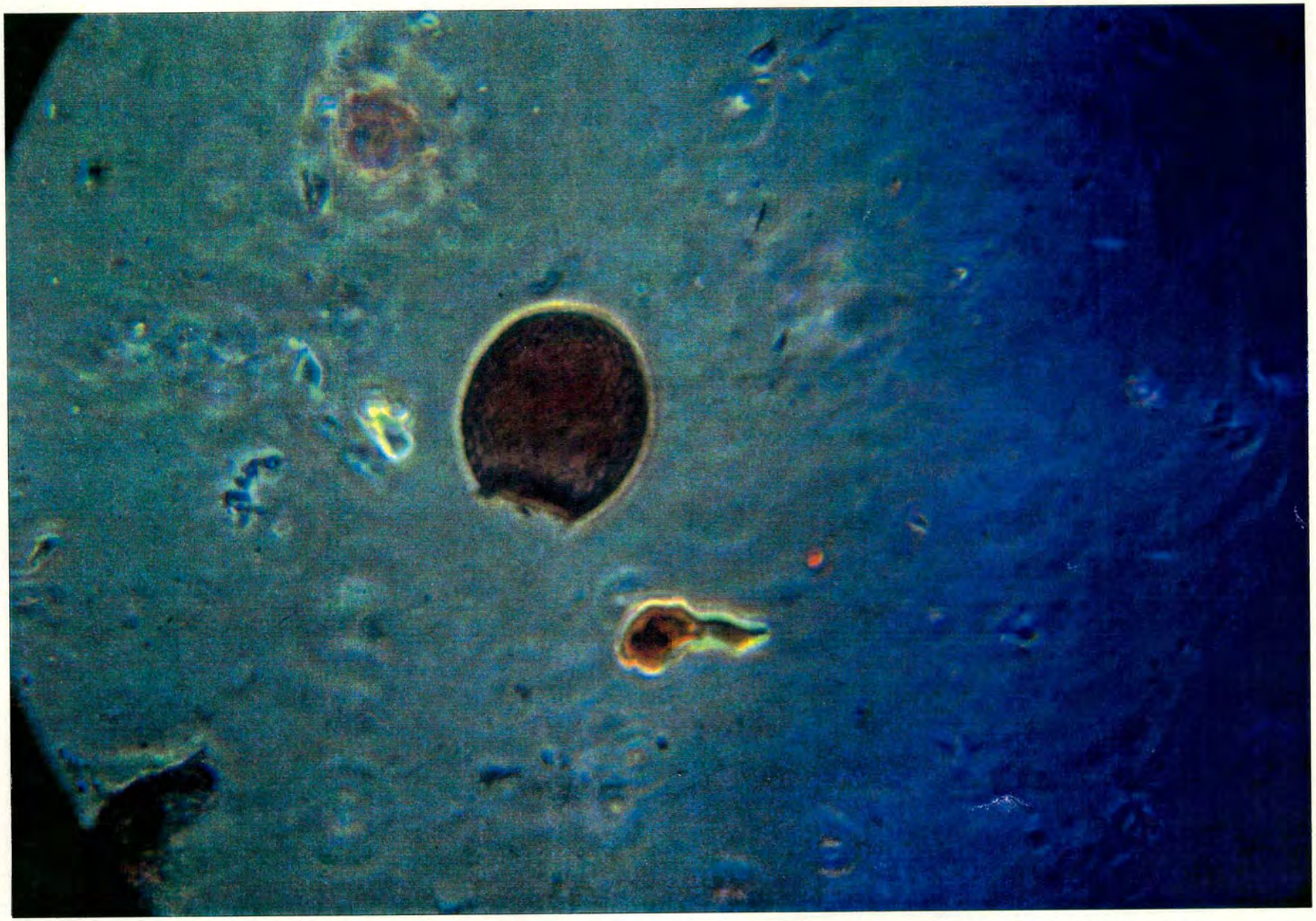

Figure II.2: *Assulina muscorum* Greef, using dark field photography at × 1000 under oil immersion on a Leitz Ortholux 2.

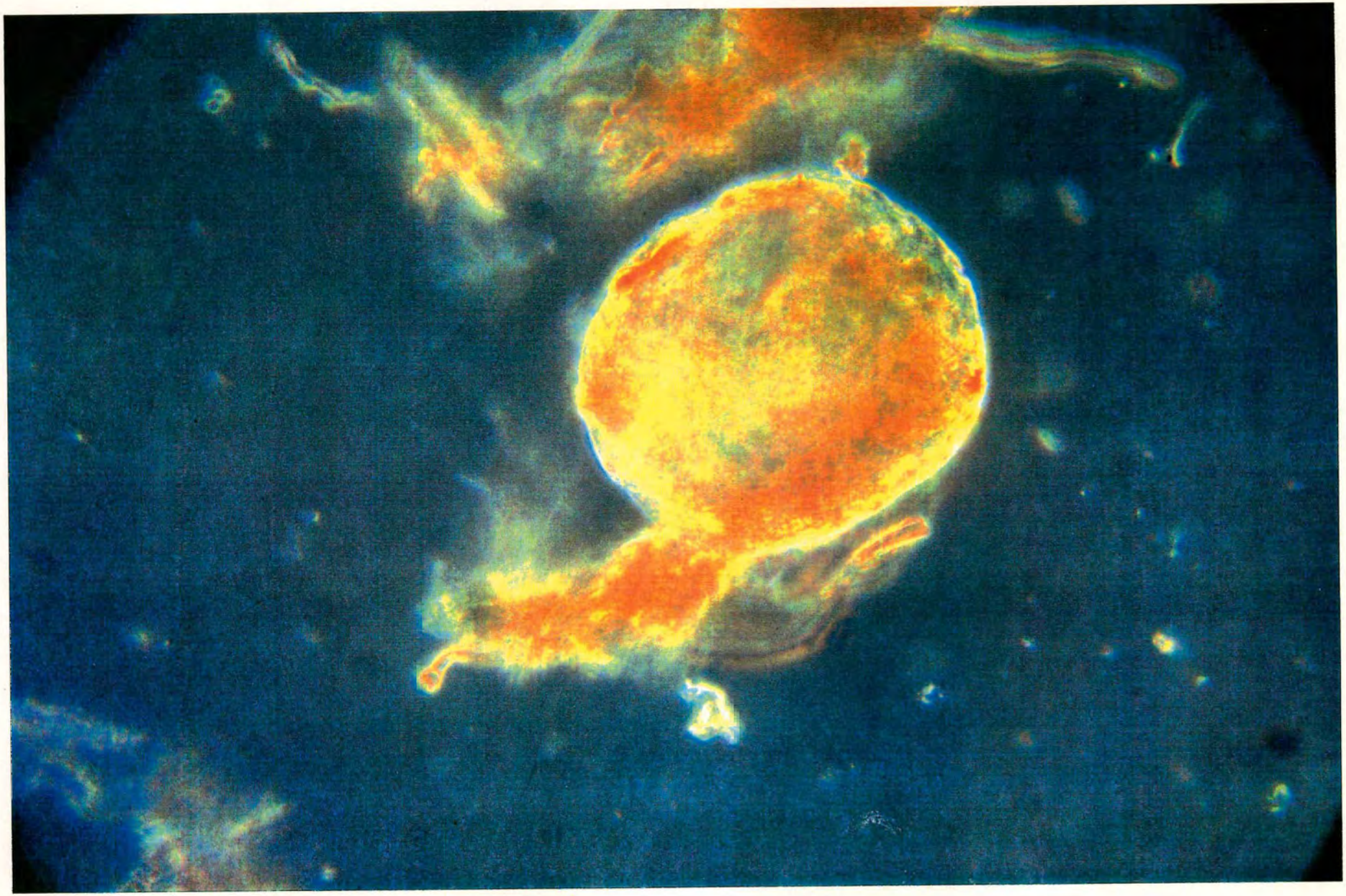

Figure II.3: Circular morph rhizopod, using dark field photography at × 1000 under oil immersion on a Leitz Ortholux 2.

specimens that have been processed for pollen counting to determine the effects of process such as acetolysis on rhizopod taxa.

(iv) Circular morph

This morph had a clear symmetrical test in which siliceous particles and a few organic particles were embedded (Figure II.3). The aperture was invaginated and surrounded by smaller siliceous particles. There were no obvious lateral pores. The lack of regular test characteristics makes agglutinate rhizopods such as this a particularly difficult group to identify (Cash & Hopkinson, 1905). From the observable features this circular taxon could belong to the *Phryganella* or *Difflugia* genera. The species description that was closest to the specimens was that of *Phryganella nidulus* Penard. This is a large species with an opaque test and an invaginated aperture. This species is hemispherical while the Creag Fhiaclach specimens were spherical. Of the *Difflugia* genus *Difflugia globulosa* Dujardin was the species whose description most closely matched the specimens. *Difflugia globulosa* differed from the circular morph in that it has a brown shell. The identification of this morph, therefore remains unclear and it was referred to throughout this thesis as the circular morph.

How can animals that are obviously motile provide a palaeoclimatic record? Studies by Heal (1962) on the response of rhizopods to reductions in moisture demonstrated that rhizopods tend to encyst rather than migrate in response to environmental stress. As rhizopods are aquatic organisms they have a physical requirement for water. In the microclimate of bryophytes where terrestrial rhizopods exist this aquatic environment is found in the water trapped between leaves and branches and stems. Moss morphology and evaprotranspiration combine to cause a vertical moisture gradient the bryophyte carpet. Larger species of rhizopod are therefore restricted to the lower layers of the bryophyte carpet, where the water film is thickest. The smaller species have the option of migrating downwards as the thickness of the water film becomes limiting. However, rhizopods will feed on other rhizopods and as the size of food particles is physically limited by the aperture size the tendency is for larger rhizopods to prey on the smaller species. Under these condition's encystment is the only evolutionarily stable strategy. The lack of migration creates the potential for rhizopods to be used as palaeoclimatic indicators. In addition, over secular time scales the bryophyte carpet at the peat surface will be reduced to much thinner deposits. This will have the effect of reducing smaller scale temporal variation in species composition.

Appendix III: Pollen preparation procedures.

Spike preparation

Pecan pollen was obtained from Park Scientific, 24 Low Farm Place, Moulton Park, Northampton, NN3 1HY. The pecan pollen suspension was made up as follows:

1. 2 g of pecan spore powder were suspended in 200 cm^3 cold 10% KOH for 36 hr to defat the grains and reduce problems of floating.
2. The suspension was centrifuged at 4,000 rpm for 10 min, and the pellet was re-suspended in distilled water and centrifuged for a second time at 4,000 rpm for 15 min.
3. This pellet was dispersed in 1000 cm^3 of 90% glycerol solution.
4. The glycerol suspension was stirred for 24 hr with an electronic stirrer.
5. Density of the suspension was checked with a Coulter counter (Edwards & Gunson, 1978). A nozzle of 75μm was used. The density of pecan grains was 4,090,000 ± 230,000 grains / cm^3 based on ten counts.

Acetolysis procedure

1. Pellet was re-suspended in glacial acetic acid.
2. Centrifuge and discard supernatant.
3. 6 cm^3 of hydrolysis mixture was added. This was a mixture glacial acetic acid and concentrated sulphuric acid in 1:9 ratio, made freshly each day.
4. Test tube was placed in a boiling water bath for 1 min.
5. Centrifuge and decant into running water.
6. Re-suspend in glacial acetic acid and centrifuge.
7. Re-suspend in water and centrifuge.

Appendix IV: Results from discriminant analysis

Table IV.1: F-to-enter values for each step in the discriminant function analysis.

Taxon	Step 0	Step 1	Step 2	Step 3	Step 4	Step 5
Pinus	36.77	36.77	26.56	29.19	26.85	36.65
Betula	8.89	3.51	3.51	3.99	6.04	10.46
Alnus	0	0	0	0	0	0
Pseu men	0	0	0	0	0	0
Calluna	19.56	0.78	0.50	0.01	0.01	0.32
Erica	0.43	0.53	0.67	0.34	6.32	6.32
Vaccinium	2.15	0.57	0.02	0.12	0.13	0.37
Empetrum	2.73	1.46	2.39	1.41	2.75	2.25
Erica UID	0	0	0	0	0	0
Juniper	0	0	0	0	0	0
Myrica	0	0	0	0	0	0
Gramineae	6.93	1.84	1.43	0.76	0.15	0.08
Cyperaceae	0	0.01	0.13	0.59	0.30	0.97
Sphagnum	1.80	0.01	0.46	0.25	0.29	1.56
Potentilla	1	1.38	1.54	0.20	0.22	0.22
Epilobium	0	0	0	0	0	0
Lyco clav	0	0.03	0.33	0.67	0.21	0.32
Diph alp	1	0.82	2.26	3.09	3.09	9.61
Sel sel	0	0	0	0	0	0
Eugl rot	2.49	0.93	3.16	1.29	1.31	0.70
Ass musc	0.05	0.01	0.01	0.56	0.50	0.44
Neb coll	1.77	0.67	0.85	0.33	0.66	0.69
C morph	1.12	3.03	3.52	3.52	4.34	3.86
Blechnum	1.00	0.03	0.01	0.06	0.12	0
Tilletia	0	0	0	0	0	0
Pediastrum	1	0	0.05	0.14	0.23	0.36
Undif	2.15	0.57	1.23	1.93	2.99	2.34

Table IV.2: Variable entered and the associated U-statistic and approximate F-statistic at each step in the discriminant function analysis.

	Step 1	Step 2	Step 3	Step 4	Step 5
Variable entered	*Pinus*	*Betula*	C morph	*Diph alp*	*Erica*
U-statistic (Wilks' Lambda)	0.43	0.38	0.34	0.30	0.24
Approximate F-statistic	36.77	21.79	17.05	14.59	15.42

Appendix V: Discriminant function calculations.

Table V.1: Samples classed as forest at 717 m, replicate four, by discriminant analysis with quotients typical of heath pollen assemblages.

Depth	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	C morph	F	H	Quotient
-1.75	-7.50	2.90	-0.60	9.37	0.00	0.00	4.17	0.75	13.58
-6.75	-7.50	5.25	-0.80	9.37	0.00	0.00	6.32	2.54	21.52
-7.75	-7.50	5.84	-0.60	9.37	0.00	0.00	7.11	1.18	24.12
-12.75	-7.50	3.78	-0.40	4.68	0.00	0.00	0.56	-0.26	17.02

Table V.2: Assemblages from replicate four, 717 m, classed as heath by discriminant analysis with quotients typical of forest pollen spectra. Two additional spectra, for which the discriminant analysis and the quotients concur are also shown.

Depth	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	C morph	H	F	Quotient
2.25	-3.40	1.45	2.89	0.00	0.00	2.50	3.44	-0.21	36.58
-10.75	-3.40	1.31	2.89	0.00	0.00	2.50	3.30	-1.12	33.24
-4.75	-3.40	1.36	2.89	0.00	0.00	0.00	0.85	1.24	34.47
-11.75	-3.40	1.49	1.45	-0.62	0.00	0.00	-1.08	0.56	38.06

Table V.3: Assemblages from replicate two 717 m, classed as heath with quotients typical of forest.

Depth	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	C morph	H	F	Quotients
-2.75	-3.40	1.63	15.93	0.00	0.00	0.00	14.16	31.71	43.54
-3.75	-3.40	1.82	15.93	0.00	0.00	0.00	14.34	32.09	48.62
-4.75	-3.40	1.96	14.47	0.00	0.00	0.00	13.03	29.47	51.20
-5.75	-3.40	1.49	14.47	0.00	0.00	0.00	12.57	28.53	42.11
-6.75	-3.40	1.77	10.12	0.00	0.00	0.00	8.49	20.39	45.00
-7.75	-3.40	1.86	2.89	0.00	0.00	0.00	1.35	6.11	44.68
-8.75	-3.40	2.06	2.89	0.00	0.00	0.00	1.55	6.49	48.37

Table V.4: Assemblages from replicate four 707 m, classed as heath with quotients typical of forest.

Depth	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	C morph	H	F	Quotients
-7.75	-3.42	1.49	5.78	0.00	0.00	0.00	3.86	1.63	44.36
-8.75	-3.42	1.00	1.45	0.00	0.00	0.00	-0.98	-1.06	32.55
-15.75	-3.42	1.49	7.23	0.00	0.00	0.00	5.30	1.43	38.68

Table V.5: Samples from the treeline core (648 m) which were classed as heath on the basis of their quotients, but as forest on the basis of the discriminant function.

Sample	Depth	Constant	*Pinus*	*Betula*	*Erica*	F	H	Quotient
170	-1.75	-7.54	6.09	0	0	-1.45	-2.51	22.04
173	-4.75	-7.54	2.88	0	4.68	0.03	-3.30	10.03
174	-5.75	-7.54	6.68	0	4.68	3.82	-2.74	23.45
175	-6.75	-7.54	7.57	0	0	0.03	-2.29	26.32
206	-8.75	-7.54	4.92	0	0	-2.62	-2.69	17.45
207	-9.75	-7.54	6.09	0	0	-1.45	-2.51	21.55
208	-10.75	-7.54	8.47	0	0	0.93	-2.15	29.81
210	-12.75	-7.54	7.27	0	0	-0.27	-2.33	25.98
235	-12.75	-7.54	4.92	-0.41	4.68	1.65	-0.11	22.56
236	5.25	-7.54	0.58	-0.41	9.37	1.99	-1.07	1.67
241	0.25	-7.54	2.88	0	4.68	0.03	-3.30	10.38
246	-4.75	-7.54	6.39	-0.41	9.37	7.81	-0.20	24.51
253	-11.75	-7.54	6.09	-0.61	4.68	2.62	1.51	23.39

Table V.6: Showing the influence of *Betula* on the classification of samples from replicate five 606 m, with quotients typical of forest.

Depth	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	C morph	H	F	Quotient
-3.75	-3.4	1.45	4.34	0.00	0	0	2.38	1.65	46.03
-6.75	-3.4	0.73	1.45	0.00	0	0	-1.22	-2.75	34.19
-9.75	-3.4	0.95	1.45	0.00	0	0	-1.00	-1.27	31.69
-11.75	-3.4	1.91	10.12	0.00	0	0	8.63	3.99	48.12

Table V.7: Showing the influence of *Betula* on the classification of samples from all replicates at 624 m with quotients typical of forest.

No	Constant	*Pinus*	*Betula*	*Erica*	*D. alp*	C morph	H	F	Quotient
94	-3.4	1.45	7.23	0.00	0	0	5.27	1.25	40.65
105	-3.4	1.40	5.78	0.00	0	0	3.78	1.15	39.74
107	-3.4	1.54	10.12	0.00	0	10	18.26	-6.77	43.47
109	-3.4	1.91	5.78	0.00	0	0	4.29	4.59	45.48
120	-3.4	1.68	5.78	0.00	0	0	4.06	3.00	39.78
122	-3.4	1.45	8.68	0.00	0	0	6.72	1.05	40.33
127	-3.4	1.82	1.45	0.00	0	5	4.86	0.43	44.75
149	-3.4	1.27	2.89	0.00	0	0	0.76	0.63	37.50
150	-3.4	1.82	5.78	0.00	0	0	4.20	3.95	58.40
152	-3.4	1.49	5.78	0.00	0	0	3.87	1.76	43.81
154	-3.4	1.54	11.57	0.00	0	0	9.71	1.27	41.46